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NORTH AMERICAN PSEUDOPHYLLIDEAN CESTODES FROM FISHES

WITH THIRTEEN PLATES

BY

ARTHUR REUBEN COOPER

Contributions from the
Zoological Laboratory of the University of Illinois
under the direction of Henry B. Ward, No. 127

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INTRODUCTION

Soon after commencing the study of *Haplobothrium globuliforme* Cooper the writer (1914, 1914a) saw that, apart from the early and somewhat brief reports and descriptions by Leidy and the later, but yet pioneer work of Linton on both marine and fresh-water species, very little had been done on the members of the order in America. Consequently the desire for an opportunity to work up other species which had in the meantime been collected at the Canadian Lake Biological Station on Georgian Bay, located at Go-Home Bay, Muskoka District, Ontario, and at the Marine Biological Station at St. Andrews, New Brunswick, grew with the feeling that something of a comprehensive nature ought to be undertaken in order not only to ascertain to what extent European species are to be found in this continent, but also to locate properly in the classification at least some of the new forms formerly described, especially by Linton. Altho the material then at hand was investigated to a certain extent at the University of Toronto, it was not until the writer came to the University of Illinois that it was studied at all thoroly with the aid of other material for comparison from the collection of the University of Illinois, under the care of Professor Henry B. Ward.

Supplementary material, which in many cases was all that was available, was obtained by Professor Ward from the United States National Museum and the Bureau of Animal Industry, but apart from a few vials no European specimens could be procured, owing to the present international conflict. On account of the lack of the latter most of the determinations have been made with the aid of the literature only, a fact which the writer feels may necessitate future changes in connection with a few species which have been more or less tentatively regarded to be the same as those in Europe. In all cases, however, the specific details of the American forms have been emphasized, so that if changes have to be made later, the basis for such will be at hand. The writer would like to point out in this connection the comparative lack from a systematic standpoint of adequate descriptions of many of the European species which have been known for many years. It was this fact which in the absence of the original material for comparison made the present work one attended with not a little difficulty.

In the main the classification of the order adopted by the writer is that proposed by Lühe (1902) and later (1910) retained with only a few modifications. The family of the Caryophyllaeidae is, however, not included, so that the order is considered to be rather that of Carus (1863), with Lühe's later conceptions of the other families. One of the latter must now again be modified considerably owing to the present study of two quite aberrant species, namely, *Haplobothrium globuliforme* Cooper and *Marsipometra hastata* (Linton) which have been found by the writer to be very disturbing to the classification.

The writer wishes here to tender his thanks in the first place to the Biological Board of Canada for placing means and facilities at his disposal in connection

with his earlier collecting at the above-mentioned Canadian Biological Stations; to the University of Illinois for the opportunity of collecting further material at the Marine Biological Laboratory at Woods Hole, Massachusetts, and at the Harpswell Laboratory, South Harpswell, Maine, during the summer of 1916, and to the staffs of these institutions as well as to that of the Marine Laboratory of the United States Bureau of Fisheries at Woods Hole for assistance and direction in connection with the same; to the Smithsonian Institute and the Bureau of Animal Industry, from whom valuable material was obtained for comparison, in the latter case thru the kind offices of Dr. C. W. Stiles of the Hygienic Laboratory, Washington; and to the following investigators for alcoholic specimens: Professor O. Fuhrmann, University of Neûchatel, Switzerland, Professor Edwin Linton, Washington and Jefferson College, Professor E. M. Walker, University of Toronto, Dr. H. J. VanCleave, University of Illinois, Dr. G. R. LaRue, University of Michigan, Dr. A. S. Pearse, University of Wisconsin, and Messrs. H. R. Hill and R. P. Wodehouse.

Finally to Professor H. B. Ward the writer wishes to express his sincere indebtedness not only for the use of his extensive private library and collections and for the procuring of rare books and specimens, but for his constant and stimulative interest in, and valuable criticism of, the work which has resulted in the following paper.

HISTORICAL DATA

Apart from Gmelin's (1790) collecting together the data given by the older writers such as Linnaeus, Pallas, Müller, Goeze, Bloch, Fabricius, Batsch, Schrank and Abildgaard, and Zeder's (1800, 1803) treatises, the first most important work on the bothriocephalid cestodes was the *Entozoorum Historia Naturalis* by Rudolphi (1808-1810). In this he reviewed the earlier literature, making valuable comments on the same, and described species of Ligula, Triaenophorus and Bothriocephalus, the latter name being used for the first time. While Lamarck (1816) dealt with only the more common species, Rudolphi in his second work of major importance, the *Entozoorum Synopsis* (1819), made some corrections of his earlier publication and further contributions in the way of a few new species. F. S. Leuckart (1819), who did not receive Rudolphi's *Entozoorum* until after his own work was in print, dealt only with species of the genus Bothriocephalus as conceived by Rudolphi, which then contained members not only of the Pseudophyllidea but also of the Tetraphyllidea and the Trypanorhyncha. Nitzsch (1824) briefly defined the species of the same genus, while later Creplin (1839) dealt with them more in detail and erected the new genus Schistocephalus. Drummond (1838) was one of the first to report bothriocephalids from the British Isles, while Bellingham (1844) and Thompson (1844) made further contributions, all three dealing with forms from Ireland. Eschricht (1841) published some of the earliest data on the internal anatomy of the group, and Kölliker (1843) made a study of the development of the eggs of a few species. The next and perhaps most important work was that by Dujardin (1845) who, while following Rudolphi in the

main, made many valuable additions from original observations. Van Beneden (1849, 1850) first essayed to erect a more comprehensive classification than had hitherto been used, and Diesing (1850) went much farther in his Subtribe I, Gymnobothria, of Tribe IV, Bothriocephalidea, of Suborder I, Aprocta, of Order IV, Cephalocotylea. Baird (1853) reverted to Rudolphi's brief system, in listing forms from the British Museum. Wagener in two papers (1854, 1857) published studies on the development which even to-day are models of careful work and excellent illustrating. Leidy (1855, 1856) was the first to report forms from America, while Weinland (1858) made a few references to bothriocephalids.

Then, until Diesing (1863) revised his classification nothing of systematic importance appeared. Olsson (1867) was one of the first to report species from the Scandinavian countries; later (1876, 1893) he made further contributions from the same region. After Willemoes-Suhm's (1869) studies on the development of *Schistocephalus dimorphus*, came Duchamp's (1876) and Donnadieu's (1877) classical experiments on the life-histories of the ligules. Linstow (1878) brought together in a list the forms known up to that time. A few years later Fraipont (1880, 1881) published studies on the excretory system of a number of species which even to-day are perhaps the most important contributions in that direction. The nervous system was made the object of special inquiry by Lang (1881), while later it was dealt with more at length by Niemiec (1888) and Cohn (1898). After a period in which such works as those with studies on development by Moniez (1881), Zschokke (1884) and Schauinsland (1885) are prominent, come the next reports of species from America, namely, those contained in Linton's first paper (1889). The latter was followed by a second (1890), containing extensions of the first, and later by others (1891, 1897, 1901 and 1901a) dealing with a variety of forms from marine and fresh-water fishes. Further anatomical studies by Lönnberg (1891), Kraemer (1892), Matz (1892) and Zernecke (1895) lead on to Monticelli's (1892) classification, which was the most important since the time of Diesing, altho Perrier (1878) had in the meantime voiced his ideas along that line. The next in order is Ariola's (1896) division of the family "Bothriocephalidae," in which incidentally were yet to be found errors regarding the position of the bothria.

Beginning with 1894 and continuing to 1900 there was in progress the publication of Braun's Cestodes in Bronn's Tierreich, which is by far the most comprehensive work on the group, since it brings together the substance of the most important of the earlier works on the morphology as well as the system of the order. One of the first papers by Lühe, who did recent important work on the group, was that (1896) in which he dealt with the nervous system of Ligula. Further study led him to publish a few years later (1899) his first classification, which was adopted by Braun (1894-1900). In the meantime Lönnberg (1897) made valuable contributions to the knowledge of the phylogeny of the parasitic flatworms; while Gamble (1896) and Perrier (1897) had erected systems of classification which, however, do not have nearly as much in their

favor for general acceptance as does that by Lühe. In 1900 Ariola brought out his revision of the family of the Bothriocephalidae, which, however, was shown by Lühe (1901) to be rather of the nature of a compilation, involving at the same time several omissions, than a distinct advance in our knowledge. In 1901 there appeared in Lankester's Treatise on Zoology Benham's classification of Cestodes which professedly follows the earlier works of Railliet and Blanchard. Lühe's (1902a) revision of the bothriocephalid system comes next in order. It is this newer system, only slightly modified in 1910, that is accepted by the writer with several necessary modifications which are dealt with below.

From 1902 until Die Süsswasserfauna Deutschlands was published, the literature on the group consists mostly of papers on individual species or mere listings. Spengel's (1905) paper on Die Monozootie der Cestoden ought, however, to be mentioned, since it is one of the latest discussions of a question which occupied a good deal of the attention of many of the older writers. Finally Ward (1910) and the writer (Cooper, 1914a, b) made the latest additions to the American literature, while Stiles and Hassall won the gratitude of the younger workers at least by their publication of the section of the Index-Catalogue of Medical and Veterinary Zoology on Subjects: Cestoda and Cestodaria which the writer has found of inestimable value in the pursuit of his studies.

EXPLANATION OF TERMS

Owing to the fact that not a little confusion exists in the earliest literature regarding the terms of orientation used for the cestode body, the writer wishes here to explain those that will be employed in the specific descriptions below.

Even much later than the time of Diesing (1850) the word "lateral" was used to refer to the flat surfaces of the typical strobila, while "marginal" was and is even yet perfectly clear in meaning; but from the standpoint of bilateral symmetry both words may mean the same thing. Here they are considered to be synonymous and are used to refer to any part which is situated in or at the edges of the strobila and consequently of the individual proglottides. On the other hand, the word "surficial" is adapted from geology to take the place of the word "flächenstandig" which is used freely in Lühe's papers to mean that the structures in question are located on the broad, flat surfaces of the chain. As is customary, the latter are considered to be dorsal and ventral in position, the ventral surface being that which is nearer the isthmus of the ovary. The end bearing the scolex is called the anterior end and the opposite, the posterior end, despite differences of opinion as to which is which. For the sake of brevity the words, "length," "depth" and "breadth" (or "width") are used instead of the longer terms, diameters in the longitudinal, in the dorsoventral and in the transverse directions, respectively, excepting where the organ in question, e.g., the transversely elongated cirrus-sac of the Triaenophorinae, is so shaped that it would be confusing to speak of its obvious length as its width. Otherwise the usual terms of orientation are employed.

KEY TO FAMILIES, SUBFAMILIES, GENERA AND SPECIES OF PSEUDOPHYLLIDEA FROM FISHES DESCRIBED IN THIS PAPER

1 (14, 15) Eggs with thick shells and opercula. Opening of cirrus and vagina on the same surface as that of the uterus and ahead of it or marginal.
Family DIPHYLLOBOTHRIIDAE Lühe 1910 . . 2

2 (11) Opening of cirrus and vagina surficial 3

3 (8) Genital openings always on the same surface of the strobila . . 4

4 (7) Scolex very short, not distinct from the strobila.
Subfamily LIGULINAE Lühe 1899 . . 5

5 (6) Segmentation confined to the anterior end, or (in larvae) absent . . . . . Ligula Bloch 1782
Type and only species: *L. intestinalis* (Linnaeus 1758) . . p. 18

6 (5) Segmentation complete even in the larval stages.
Schistocephalus Creplin 1829
Type and only species.
Schistocephalus solidus (O. F. Müller 1776) . . . . p. 30

7 (4) Scolex (secondary, see below) similar in shape to the first proglottis; no neck; segmentation beginning immediately behind the scolex, but confined to the anterior end of the worm.
Subfamily HAPLOBOTHRIINAE Cooper 1917 . . p. 42
Type and only genus . . Haplobothrium Cooper 1914 . . p. 43
Type and only species: *H. globuliforme* Cooper 1914 . . p. 44

8 (3) Genital openings of different segments not on the same surface, but alternating irregularly from one surface to the other. External segmentation little expressed.
Subfamily CYATHOCEPHALINAE Lühe 1899 . . 9

9 (10) Scolex an unpaired, terminal, funnel-shaped organ.
Cyathocephalus Kessler 1868
Only American species: *C. americanus* Cooper 1917 . . p. 53

10 (9) Scolex with two almost spherical bothria, the apertures of which may be separated or more or less completely fused to form a single terminal opening . . . . Bothrimonus Duvernoy 1842
Only American species: *B. intermedius* Cooper 1917 . . p. 63

11 (2) Opening of cirrus and vagina marginal.
Subfamily TRIAENOPHORINAE Lühe 1899 . . 12

12 (13) Scolex armed with four three-pointed hooks.
Triaenophorus Rudolphi 1793
Only larval forms of two specific types present . . . . . p. 82

13 (12) Scolex sagittate, or replaced by a pseudoscolex. Segmentation strongly expressed, the individual proglottides very short with leaf-like free lateral portions . . . . . Fistulicola Lühe 1899
Only American species: *F. plicatus* (Rudolphi 1819) . . . p. 89

14 (1, 15) Eggs with thin shells and no opercula. Opening of cirrus and vagina marginal, that of uterus at the same level or slightly behind it and ventral. Segmentation very distinct and regular.
Subfamily MARSIPOMETRINAE Cooper 1917 . . p. 70
Type and only genus: Marsipometra Cooper 1917 . . p. 70
Type and only species: *M. hastata* (Linton 1898) . . p. 71

15 (1, 14) Eggs with thin shells and no opercula. Opening of cirrus and vagina dorsal and behind the ventral uterus-opening, or marginal in which case sementation is not well expressed.
Family PTYCHOBOTHRIIDAE Lühe 1902 . . 16

16 (27) Opening of cirrus and vagina surficial.
Subfamily PTYCHOBOTHRIINAE Lühe 1899 . . 17

17 (26) Scolex elongated, with prominent terminal disc. Segmentation well developed, neck absent.
Bothriocephalus Rudolphi 1808 . . 18

18 (23) Scolex not pronouncedly constricted posteriorly 19

19 (20) Uterus-sac occupies one-sixth of the transverse diameter of the proglottis . . . . . *B. scorpii* (Müller 1776) . . p. 96

20 (19) Uterus-sac occupies one-third of the transverse diameter of the proglottis 21

21 (22) Scolex small . . . . . *B. claviceps* (Goeze 1782) . . p. 114

22 (21) Scolex large, terminal disc deeply notched surficially, sagittate in lateral view . . . . . *B. cuspidatus* (Cooper 1917) . . p. 123

23 (18) Scolex constricted posteriorly 24

24 (25) Terminal disc deeply notched laterally as well as surficially; vagina provided with a bulbous sphincter near its opening . . . . . .
. . . . *B. manubriformis* (Linton 1889) . . p. 133

25 (24) Terminal disc rectangular; no vaginal sphincter . . . . . .
. . . . . *B. occidentalis* (Linton 1898) . . p. 149

26 (17) Scolex almost spherical; walls of each bothrium fused to form a hollow organ of attachment with a small anterior opening
Clestobothrium Lühe 1899
Type and only species: *C. crassiceps* (Rudolphi 1819) . . p. 154

27 (16) Opening of cirrus and vagina marginal.
Subfamily AMPHICOTYLINAE Lühe 1902 . . 28
Onlygenus represented . . . . . Abothrium van Beneden 1871.

28 (29) Pseudoscolex in adult. Longitudinal muscles in bundles. Vitelline follicles entirely within the longitudinal muscles.
A. rugosum (Batsch 1786) . . p. 172

29 (28) Scolex typical, but variously shaped. Longitudinal muscles not in bundles. Vitelline follicles among the longitudinal muscles or outside of them . . . . . *A. crassum* (Bloch 1779) . . p. 186

Order PSEUDOPHYLLIDEA Carus 1863, nec Lühe 1910, e. p.

Polyzootic cestodes with mostly unarmed scolex without rostellum or proboscis formation, excepting in the Haplobothriinae where the primary scolex is provided with four protrusible proboscides resembling those of the Trypanorhyncha. Usually with two weakly developed sucking grooves, which in individual cases are modified by the strong development of their walls or by more or less extensive fusion of their edges, so that they may appear funnel-shaped or tubular, which may also unite with each other more or less completely to form an unpaired terminal adhesive organ, or become rudimentary or entirely absent, in which latter case they are replaced by a terminal functional organ of attachment. The development of a pseudoscolex takes place occasionally. External segmentation more or less pronounced, only seldom completely absent. Genitalia in each segment usually single, seldom double. Their development proceeds from ahead backwards and does not continue to a degeneration of the reproductive glands; but the majority of the proglottides, being at the same stage of development, bring their sexual products to maturity at the same time, so that in all of them new eggs are formed continuously and all the eggs of the whole animal are at the same stage of embryonic development. A surficial opening of the uterus is always present.

Testes numerous; vas deferens strongly coiled, without a true seminal vesicle. Ovary near the posterior end of the proglottis, mostly median in the case of single genitalia, seldom approaching the margin of the strobila bearing the genital opening (that of the cirrus and vagina). Vitelline follicles very numerous, mostly in the cortical, seldom in the medullary parenchyma. Uterus a more or less winding canal, the individual coils of which converge somewhat towards the centre of the proglottis to form the so-called rosette; but in other forms it enlarges to form a capacious cavity, the uterus-sac, from which the duct-like beginning of the uterus is sharply separated. Eggs operculate or non-operculate, developing mostly only after being laid, but in other cases within the uterus.

The above diagnosis of the order is that of Lühe (1910:11), minus the family Caryophyllaeidae and partly emended to accommodate the subfamily Haplobothriinae, in which what is here considered to be the true (or primary) scolex is deprived of bothria but provided with four eversible proboscides quite comparable in structure to those of the order Trypanorhyncha. It is evident that what was formerly (Cooper, 1914, 1914a) called the scolex of Haplobothrium cannot now be considered to be a true scolex but only the foremost segment of the adult or secondary strobila, which is indicated by its resemblance internally as well as externally to the segments immediately following. Whether or not a pair of bothria were originally present or are present in the very earliest stages, whether such bothria have become modified into the proboscides, or whether the latter have developed from four separate "accessory

suckers" as believed by Pintner (1880) to be the case in the Trypanorhyncha, must remain mere suggestions for the present. Furthermore as to the formation of segments there are in Haplobothrium not only conditions quite similar to those in Bothriocephalus *s. str.* and other genera in which there is no neck, segmentation beginning immediately behind the scolex, but those reminding one of the proliferation of scolices in echinococcus. In the former, as will be seen below where the process is described more in detail (p. 102), a primary segment divides up into secondary segments, these into tertiary segments, and so on until there may be eventually thirty-two or more genital segments corresponding to one primary segment formed immediately behind the scolex. In Haplobothrium a primary strobila divides up into primary segments, these subdivide into secondary segments, the definitive joints of the ordinary strobila met with, which in turn may be subdivided again and evidently indefinitely to form new chains. The chief difference between these two cases is one of degree of regularity in the subdivision. Whereas in Bothriocephalus the whole anterior region of the worm is affected, evidently no division taking place after the rudiments of the reproductive organs have become separated from the common rudiment, and the subsegments remain attached to one another, in Haplobothrium not only do the primary segments separate as secondary strobilas, but in the latter only a limited region is involved in further subdivision. On the other hand there is somewhat of a resemblance between this manner of subdivision in Haplobothrium and that of the larval Echinococcifer in that the strobilas are developed from an original "nurse." That is, the primary strobila of the former might be looked upon as a nurse from which are developed segments, comparable to the daughter-cysts of an echinococcus, which in turn produce (secondary) scolices and eventually strobilas. In other words there might be recognized at first sight a sort of alternation of generations in the case of Haplobothrium. But this comparison is only a superficial one, for as will be shown below (under Haplobothriinae) the secondary scolex cannot be considered to be a true scolex nor the secondary strobila a true strobila; but the primary strobila with its four proboscides must be regarded as such. Finally, this peculiar method of segmentation reminds one of the asexual budding of some of the oligochaete worms, particularly as regards the proliferation of subsegments in the anterior region of the first formed divisions; but further than this the comparison can scarcely be carried.

DIPHYLLOBOTHRIIDAE Lühe 1910, char. emend.

Polyzootic Pseudophyllidea with unarmed or (seldom) armed scolex. Surficial bothria variously developed; they may be modified to form sucking tubes, each with an anterior and a posterior opening, thru the growth together of their free edges, or an unpaired terminal organ of attachment can serve as a functional substitute for the rudimentary bothria or result from the more or less complete fusion of both bothria. The whole scolex may be replaced in sexually mature specimens by a pseudoscolex; or it may be (Haplobothriinae) provided with four protrusible proboscides. Neck present or absent. External segmentation mostly present, seldom absent. Genital organs numerous, mostly single in each proglottis, seldom double. Cirrus unarmed (excepting in Haplobothrium), with cleft cuticula. Opening of cirrus and vagina surficial or marginal; in the first case always on the same surface as the uterus opening and ahead of this as well as always in the median line of the genital complex, also in the median line of the proglottis in the case of single genitalia. Both surfaces of the chain of proglottides, apart from the genital openings, similarly shaped. Receptaculum seminis formed by a local enlargement of the vagina near its inner end, which as a rule is sharply separated from the spermiduct (terminal portion of the vagina). Uterus, a long, more or less winding canal, usually in the form of a rosette, formed by almost transversely directed coils crossing the median line. It may be locally more or less enlarged, but seldom forms an undivided uterus-sac distinct from the uterine duct, as in the Ptychobothriidae. Eggs thick shelled, with opercula, excepting in the Marsipometrinae; their formation is carried on continuously in fully-developed proglottides; embryonal development takes place usually after liberation, seldom in the uterus, in which case, however, all stages are found side by side.

Parasites of vertebrates.

Lühe's (1910:16) diagnosis is here emended to include the new subfamilies Haplobothriinae and Marsipometrinae. In the former not only is the scolex radically different from that of any other member of the family, but the cirrus is armed with minute spines and there is a distinct uterus-sac, separate from the uterine duct as in the Ptychobothriidae; while in the latter there is likewise a uterus-sac and the eggs are not provided with opercula. The cirrus of Haplobothrium, however, would seem to exclude the genus from the family Ptychobothriidae as well as from the Diphyllobothriidae, since it is not "unarmed, with cleft cuticula," but provided with minute yet distinct cuticular spines bearing some resemblance to those of the Acanthophallidae (Amphitretidae), as pointed out elsewhere by the writer (1914:3). But *H. globuliforme* is otherwise so nearly related to *Diphyllobothrium latum* that it does not seem wise to remove it from the family on this account, especially since these spines are so minute and since the evidence points to their being probably of little, if any, functional importance. The uterus on the other hand is quite diff-

erent from that of any of the members of this family in that it is distinctly divided into uterine duct and uterus-sac as in the Ptychobothriidae. It is true that in the genus Scyphocephalus one or two of the coils of the uterine rosette becomes much enlarged when the organ is filled with eggs, while in Bothridium, as stated by Lühe (1899:49), "Der Uterus bildet keine Rosettenform, lässt jedoch Uteringang und Uterus s. str. deutlich unterscheiden; letzterer stellt gewissermassen eine zweitheilige Uterushöhle dar, indem zwei hinter einander gelegene grosse Hohlräume durch einen kurzen und dünnen Canal miteinander in Verbindung stehen." But in neither case is there a single uterus-sac, distinct and separate from the uterine duct or beginning of the uterus, but only a modified rosette formation. Roboz (1882:282) in describing the development of the uterus of *Bothridium pithonis* said that: "In dieser Weise ist er natürlich nur in jüngeren Gliedern entwickelt, während er dort, wo die Befruchtung schon beendet ist, in Folge der immer stärkeren Ansammlung von den mit chitinöser Hülle umgebener Eiern immer grösser wird und sich schliesslich zu einem die ganze Mittelschicht ausfüllenden Sack ausbreitet." It would thus seem to be comparable to that of the Ptychobothriidae in that its functional sac is developed by a distal enlargement of the original duct which gradually encroaches upon the medulla, but evidently there is no separation of the organ into two distinct parts at any stage as there is in Haplobothrium. And, as emphasized elsewhere by the writer, this separation is present at all stages in the development of the organ, which as a matter of fact proceeds in quite the same manner as that of Bothriocephalus. In Marsipometra, on the other hand, even tho the sac is formed in the same way, it is never very sharply separated from the uterine duct, altho such appears to be the case in the adult. Reference to the specific description below will elucidate this latter point. Finally as regards the fact that its eggs are not provided with opercula, Marsipometra stands alone. This character would place it at once in the Ptychobothriidae, but it is otherwise so closely related to the subfamily Triaenophorrinae that the family is here emended to accommodate it. Thus it is seen that on account of these two isolated genera the two families Diphyllobothriidae and Ptychobothriidae are much more closely related than was formerly thought to be the case.

LIGULINAE Lühe 1899

Scolex unarmed, very short, almost triangular, with anterior end, more or less drawn out into a point according to the state of contraction, passing directly into the chain of proglottides or the similarly shaped unjointed body; surficial bothria small, weakly developed. Neck absent. Formation of proglottides complete, confined to the anterior end or (in young animals) absent. Posterior end rounded. Nervous system distinguished by a large number of plexus-forming longitudinal nerves near both chief strands. Genital organs in sexually mature individuals completely developed close behind the scolex. Genital openings surficial, ventral, lying behind or near one another and near the median line. Testes in a simple dorsal layer in the lateral fields of the medul-

lary parenchyma, for the most part lateral to the nerve strands. Ovary and shell-gland median, the former ventral, the latter dorsal. Vitelline follicles in the form of a mantle in the cortical parenchyma. Vas deferens enlarged to a muscular bulb before entering the cirrus-sac. Receptaculum seminis large, sharply separated from the short and narrow spermiduct.

Sexually mature in the intestines of water birds; present as larvae in the body-cavities of teleosts where they grow quite large and develop the rudiments of the reproductive organs; occasionally also observed free in the water which they reach by the rupture of the greatly distended body-wall of the intermediate host.

Type genus: Ligula Bloch

In the above diagnosis of the subfamily by Lühe (1910:17) the statement that the testes are "in einfacher dorsaler Schicht den Seitenfeldern des Mark-parenchyms grossentheils lateralwärts von den Markströngen" is somewhat confusing, for it is strictly correct only when the whole number of testes is taken into consideration. In transections of both Ligula and Schistocephalus the nerve strand was actually found to be more than half way from the median line to the margin of the medulla, but the testes were much more closely crowded in the lateral portion of the field, hence making their total number there more than in the median field. But the differences between the two fields on each side in this regard were seen in confirmatory frontal sections to be much greater in Ligula than in Schistocephalus.

LIGULA Bloch 1782

Taenia (part.)	Auctorum	
Fasciola (part.)	Linnaeus	1758
Fasciola (part.)	Linnaeus	1767
Ligula	Bloch	1782
Fasciola (part.)	Goeze	1782
Bothriocephalus (part.)	Nitzsch	1824
Ligula	Creplin	1839
Dibothrium (part.)	Donnadieu	1877

Bothria as well as external segmentation completely absent from the larvae, both develop simultaneously with the maturation of the sex-organs in the definitive host, where the external segmentation which does not correspond with the internal is confined to the anterior end. Longitudinal and transverse muscles irregularly interwoven in the anterior end, posteriorly separated into an inner transverse and an outer longitudinal layer.

Type (and only) species: *Ligula intestinalis* (L.).

LIGULA INTESTINALIS (Linnaeus 1758)

[Figs. 1, 2, 78, 98]

LARVAL STAGE:

1713	Taenia	Geoffroy	1713 : 50
1740	*Taenia capitata*	Frisch	1740 : 121
1758	*Fasciola intestinalis*	Linnaeus	1758 : 649
1767	*Fasciola intestinalis*	Linnaeus	1767 : 1078
1781	*Taenia cingulum*	Pallas	1781 : 95
1782	*Ligula piscium*	Bloch	1782 : 2
1782	*Fasciola abdominalis*	Goeze	1782 : 187
1790	*Ligula abdominalis*	Gmelin	1790 : 3043
1790	*Ligula a. alburni*	Gmelin	1790 : 3043
1790	*Ligula a. bramae*	Gmelin	1790 : 3043
1790	*Ligula a. carassii*	Gmelin	1790 : 3043
1790	*Ligula a. cobitidis*	Gmelin	1790 : 3043
1790	*Ligula a. cyprinorum*	Gmelin	1790 : 3043
1790	*Ligula a. gobionis*	Gmelin	1790 : 3043
1790	*Ligula a. leuscisci*	Gmelin	1790 : 3043
1790	*Ligula a. trincae*	Gmelin	1790 : 3043
1790	*Ligula a. vimbae*	Gmelin	1790 : 3043
1790	*Ligula petromyzontis*	Schrank	1790 : 119
1793	*Ligula salvelini*	Schrank	1793 : 143
1802	*Ligula simplicissima*	Rudolphi	1802 : 99
1803	*Ligula alburni*	Zeder	1803 : 266
1803	*Ligula bramae*	Zeder	1803 : 263
1803	*Ligula carassii*	Zeder	1803 : 262–3
1803	*Ligula cobitidis*	Zeder	1803 : 266
1803	*Liguli colymbi*	Zeder	1803 : 266
1803	*Ligula gobionis*	Zeder	1803 : 265
1803	*Ligula leucisci*	Zeder	1803 : 265
1803	*Ligula trincae*	Zeder	1803 : 265
1803	*Ligula vimbae*	Zeder	1803 : 295
1810	*Ligula acuminata*	Rudolphi	1810 : 24
1810	*Ligula cingulum*	Rudolphi	1810 : 20–22, 31
1810	*Ligula constringens*	Rudolphi	1810 : 22–24
1810	*Ligula contortrix*	Rudolphi	1810 : 18–19
1819	*Ligula simplicissima*	Rudolphi	1819 : 134
1819	*Ligula crispa*	Rudolphi	1819 : 134–135
1819	*Ligula edulis*	Briganti	1819 : 209
1839	*Ligula simplicissima*	Creplin	1839 : 295
1839	*Ligula monogramma*	Creplin	1839 : 296
1839	*Ligula digramma*	Creplin	1839 : 296
1853	*Ligula simplicissima*	Baird	1853 : 95
1855	*Ligula monogramma*	Leidy	1855 : 444
1861	*Ligula monogramma*	Van Beneden	1861 : 139
1891	*Ligula catostomi*	Linton	1891 : 66
1896	*Ligula monogramma*	Zschokke	1896 : 773, 774, 775
1898	*Dibothrium ligula*	Linton	1898 : 438
1899	*Ligula abdominalis*	Lühe	1899 : 52

ADULT STAGE:

1782	*Ligula avium*	Bloch	1782 : 4
1782	*Fasciola intestinalis*	Goeze	1782 : 183

ADULT STAGE

1790	*Ligula intestinalis*	Gmelin	1790 : 3042
1802	*Ligula simplicissima*	Rudolphi	1802 : 99
1803	*Ligula colymbi*	Zeder	1803 : 266
1810	*Ligula uniserialis*	Rudolphi	1810 : 12
1810	*Ligula alternans*	Rudolphi	1810 : 13
1810	*Ligula interrupta*	Rudolphi	1810 : 15
1810	*Ligula sparsa*	Rudolphi	1810 : 16
1819	*Ligula uniserialis*	Rudolphi	1819 : 132
1819	*Ligula alternans*	Rudolphi	1819 : 133
1819	*Ligula interrupta*	Rudolphi	1819 : 133
1819	*Ligula sparsa*	Rudolphi	1819 : 133
1824	*Bothriocephalus semiligula*	Nitzsch	1824 : 98
1839	*Ligula uniserialis*	Creplin	1839 : 296
1839	*Ligula interrupta*	Creplin	1839 : 296
1844	*Ligula sparsa*	Bellingham	1844 : 165
1845	*Ligula uniserialis*	Dujardin	1845 : 628
1845	*Ligula alternans*	Dujardin	1845 : 629
1845	*Ligula interrupta*	Dujardin	1845 : 629
1845	*Ligula sparsa*	Dujardin	1845 : 629
? 1845	*Ligula nodosa*	Dujardin	1845 : 629
1850	*Ligula monogramma*	Diesing	1850 : 579
1850	*Ligula digramma*	Diesing	1850 : 580
1853	*Ligula interrupta*	Baird	1853 : 96
1853	*Ligula sparsa*	Baird	1853 : 96
1854	*Ligula monogramma*	Diesing	1854 : 19
1854	*Ligula digramma*	Diesing	1854 : 18
? 1856	*Ligula reptans*	Leidy	1856 : 46
1863	*Ligula monogramma*	Diesing	1863 : 230
1863	*Ligula digramma*	Diesing	1863 : 231
1870	*Ligula monogramma*	Willemoes-Suhm	1870 : 94
1877	*Dibothrium ligula*	Donnadieu	1877 : 495
1881	*Ligula simplicissima*	Moniez	1881 : 37, 81
1882	*Ligula simplicissima*	Kiessling	1882
1884	*Dibothrium ligula*	Zschokke	1884 : 26
1885	*Ligula simplicissima*	Schauinsland	1885 : 550
1888	*Ligula simplicissima*	Niemiec	1888 : 2
1893	*Ligula monogramma*	Olsson	1893 : 15
1894	*Ligula simplicissima*	Stiles and Hassall	1894 : 331
1895	*Ligula monogramma*	Zernecke	1895 : 93
1895	*Ligula digramma*	Zernecke	1895 : 93
1896	*Ligula simplicissima*	Zschokke	1896 : 773, 774, 775
1898	*Ligula digramma*	Cohn	1898 : 134
1898	*Ligula uniserialis*	Lühe	1898 : 286
1898	*Ligula uniserialis*	Muehling	1898 : 32
1898	*Ligula monogramma*	Stossich	1898 : 118
1899	*Ligula intestinalis*	Lühe	1899 : 52
1900	*Ligula avium*	Braun	1900 : 1687
1900	*Ligula uniserialis*	Wolffhuegel	1900 : 63
1901	*Ligula intestinalis*	Linstow	1901a
1902	*Ligula monogramma*	Parona	1902 : 7
1902	*Ligula intestinalis*	Schneider	1902a : 13
1903	*Ligula intestinalis*	Linstow	1903 : 20
1910	*Ligula intestinalis*	Lühe	1910 : 18

Specific diagnosis: With the characters of the genus. Large worms from 100 to 1000mm. in length by 5 to 15mm. in breadth. Anterior end rounded, protruding; bothria faint. Strobila greatly elongate, depressed, maximum breadth anterior to the middle, gradually tapering to the posterior end. Body crossed by irregular ridges and furrows, and wavy at the margins in the adult, with 35 to 40 external segments anteriorly. Deep median groove on each surface in the larva, two very shallow parallel grooves near the median line on the dorsal surface in the adult.

Cuticula 5 to 20μ in thickness, subcuticula 50 to 110μ. Nerve strands 50 to 100μ in diameter. Excretory vessels numerous in three layers, one close beneath, among or just outside of the vitelline glands (cortical), another among the main body muscles, and a third in the medulla.

Genitalia from 0.05 to 0.20mm. apart. Genital cloaca a narrow transverse slit, 0.18 to 0.20 by 0.02 to 0.03mm. into which open separately the cirrus, uterus, and vagina, the latter constantly between the other two which alternate irregularly from side to side.

Testes interrupted only medially, 20 to 40 in transection, 115 to 145 by 80 to 85 by 45 to 55μ in dimensions. Vas deferens up to 35μ in diameter, loosely coiled above the cirrus-sac. Seminal vesicle small, close above the latter, 65 to 100 by 40 to 90μ. Cirrus-sac somewhat lateral, ovoid, with thin walls, 185 to 215 by 130 to 160 by 130 to 145μ. Cirrus proper within cirrus-sac, long and coiled, 25μ in diameter.

Vagina 15 to 30μ in diameter, receptaculum seminis 75 to 90μ. Spermiduct short, 20 to 25 by 6 to 12μ. Ovary 0.5 to 1.5 mm. in diameter; wing greatly depressed, isthmus prominent and not in the median line but alternating irregularly from side to side opposite the cirrus-sac; ova in same 12 to 15μ in diameter. Oocapt 18 to 20μ in diameter, oviduct 15 to 20μ. Vitelline reservoir ellipsoidal in shape, sharply separated from the duct on either side, 40 by 30μ. Vitelline follicles irregular in shape, 50 to 70 by 15 to 30μ, in a layer close beneath the subcuticula and broken only ventrally. Shell-gland composed of much elongated cells with enlarged bodies and narrow necks connecting with the oviduct for 30μ of its length. Uterus a mass of coils in the median line, 0.4 to 0.6mm. in diameter, that of the tube being 30 to 60μ.

Eggs, 50 to 65 by 30 to 42μ.

Habitat: As larvae in the body-cavities of teleosts; adults in the intestines of wading and diving birds.

HOST	LOCALITY	COLLECTOR	AUTHORITY
Larval stage:			
Leuciscus rutilis	.....	Zschokke	Zschokke 1884 : 26
Abramis brama	East Prussia	Schauinsland	Muehling 1898 : 33
Cyprinus alburnus	Berlin	Goeze	Goeze 1782 : 187
Aspius rapax	Iljmen-See, Novogorod	Varpachovskij	Linstow 1903 : 285
Gobio vulgaris	.....	Rudolphi	Diesing 1850 : 581
Carrassius gibelio	.....	Rudolphi	Diesing 1850 : 581
Petromyzon branchialis	.....	Schrank	Rudolphi 1810 : 24
Cobitis taenia	.....	Bloch	Rudolphi 1819 : 134
Salmo salvelinus	.....	Schrank	Diesing 1850 : 581
Coregonus wartmanni	.....	Schrank	Diesing 1850 : 581
Siluris glanis	.....	Mus. Vienna	Diesing 1850 : 581
Esox lucius	Sweden	Olsson	Olsson 1893 : 15
Perca fluviatilis	L. Storsjön, Jemtland, and Bönan, Sweden	Olsson	Olsson 1893 : 15
Lucioperca sandra	.....	Mus. Vienna	Diesing 1850 : 581
?Phoca vitulina	Berlin	Rudolphi	Rudolphi 1819 : 135
Morrhua americana	.....	Schafirt	Leidy 1855 : 444
Squalius cephalus	.....	Zschokke	Zschokke 1884 : 26
Alburnus lucidus	Langviken Bay, Finland	Levander	Schneider 1902a : 13
Atherina mocho	Cagliari	Parona and Mazza	Parona and Mazza 1900 : 233
Blicca bjorkna	.....	Linstow	Linstow 1901a : 629
Catostomus ardens	Yellowstone Nat. Park	D. S. Jordan	Linton 1891 : 65
Chondrostoma nasus	Basel	Zschokke	Zschokke 1896 : 775
Catostomus latipinnis	Gila R. and Salt R., Arizona	E. Palmer	Linton 1898 : 438
Osmerus mordax	Potomac R., Hagerstown, Md.	C. E. Ridenour	Linton 1898 : 438
Hybognathus nuchalis	.....	.....	Linton 1898 : 438
Notropis cornutus	Fourth Lake, Adirondacks, New York	F. Mather	Linton 1898 : 438
Schizopygopsis kozlovi	Tan-la-Gebirge, Tibet	Przevalskij	Linstow 1903 : 285
Nemachilus strauchi	Issyk-kul-See, Bai Karasu	P. Schmidt	Linstow 1903 : 285
Tinca vulgaris	.....	.....	Neveu-Lemaire 1909 : 88
Gobio gobio	.....	.....	Lühe 1910 : 19
Scardinius erythrophthalmus	.....	.....	Lühe 1910 : 19
Ameiurus sp.	Charlevoix,	H. B. Ward	Cooper (the present paper)
Alosa ohiensis	Keokuk, Iowa	H. B. Ward	"
Perca fluviatilis	Walnut Lake, Michigan	H. B. Ward	"

HOST	LOCALITY	COLLECTOR	AUTHORITY	
Perca flavescens	Go-Home Bay, Muskoka District, Ontario	A. R. Cooper	"	
Catostomus commersonii	Walnut Lake, Michigan	H. B. Ward	"	
Catostomus commersonii	Douglas Lake, Michigan	H. R. Hill	"	
Catostomus commersonii commersonii	Douglas Lake, Michigan	A. R. Cooper	"	
Notropis cornutus	Go-Home Bay	A. R. Cooper	"	
Notropis cayuga	Douglas Lake, Michigan	H. R. Hill	"	
Notropis hudsonius	Douglas Lake, Michigan	G. R. LaRue	"	
Micropterus dolomieu	Go-Home Bay	A. R. Cooper	"	
Ambloplites rupestris	Go-Home Bay	A. R. Cooper	"	
Ambloplites rupestris	Douglas Lake, Michigan	G. R. LaRue	"	
Gasterosteus bispinosus atkinsii	Chamcook Lake, New Brunswick	A. R. Cooper	"	
Ambystoma sp.	Sand Hills, Nebraska	G. R. LaRue	"	
Ambystoma tigrinum	Cherry Co., Nebraska	G. R. LaRue	"	
Free on shore	Douglas Lake, Michigan	H. R. Hill	"	
		G. R. LaRue	"	
		A. R. Cooper	"	
Adult stage:				
Falco albicilla	Greiphswald	Creplin	Creplin	1839 : 296
Ciconia alba	....	Hildebrandt	Diesing	1850 : 580
Ardea nycticorax	.....	M. C. V.	Diesing	1850 : 580
Colymbus arcticus	.....	Mehlis	Diesing	1850 : 581
Podiceps auritus	Varese	Parona	Parona	1902 : 7
Anas boschas fera	.....	Mus. Vienna	Rudolphi	1819 : 134
Larus argentatus	Kainsk, Enissej	Middendorff	Linstow	1903 : 20
Sterna hirundo	.....	Mus. Vienna	Rudolphi	1819 : 133
Mergus serrator	Gulf of Finland	Schneider	Schneider	1902a : 13
Nycticorax nycticorax	.....	.....	Lühe	1910 : 18
Graculus carbo	.....	M. Siebold, Coll. Brit. Museum	Baird	1853 : 96
Fuligula clangula	Jemtland	Olsson	Olsson	1893 : 15
Xema minutum	Trieste	Stossich	Stossich	1898 : 118
Urinator arcticus	....	.....	Lühe	1900 : 18
Rissa tridactyla	.....	.....	Lühe	1900 : 18
Stercorarius parasitica	.....	.....	Lühe	1900 : 18
Hydrochelidon nigra	.....	.....	Lühe	1910 : 18
Herodias alba	.....	.....	Lühe	1910 : 18
Haliaetus albicilla	.....	.....	Lühe	1910 : 18

HOST	LOCALITY	COLLECTOR	AUTHORITY
Aquila chrysaetus	.....	.....	Lühe 1910 : 18
Corvus cornix	.....	.....	Lühe 1910 : 18
Podilymbus podiceps	.....	H. B. Ward	Cooper (the present paper)
Merganser sp.	Urbana, Illinois	H. B. Ward	"
Colymbus hoelbeelli	.....	H. B. Ward	"
Mergus merganser	Douglas Lake, Michigan	G. R. LaRue	"

The species has also been reported in Europe and Asia from the following additional hosts:

Larval stages: *Abramis bjorkna, A. blicca, A. vimba, Alburnus alburnus, Ammocoetes branchialis, Aspius alburnus, Carassius carassius, C. vulgaris, Cobitis aculeata, Cyprinus blicca, C. brama, C. carassius, C. gobio, C. lacustris, C. leuciscus, C. tinca, Gobio fluviatilis, Leuciscus erythrophthalmus, L. leuciscus, L. phoxinus, L. pulchellus, L. vulgaris, Lucioperca lucioperca, Squalius turcicus.*

Adult stages: *Ardea alba, A. ciconia, A. egretta, Ciconia ciconia, C. nigra, Colymbus auritus, C. cristatus, C. griseigena, C. rubricollis, C. septentrionalis, C. subcristatus, Falco chrysaetos, F. fulvus, Larus canus, L. melanocephalus, L. parasiticus, L. pelecanus carbonis, L. pygmaei, L. ridibundus, L. tridactylus, Mergus albellus, M. merganser, M. minutus, Podiceps minor, P. nigricollis, P. rubricollis, Sterna nigra, Totanus chloropus, Urinator stellatus, Xema ridiundum.*

As indicated in the above synonymy, the greatest confusion has existed in connection with this species from the time of Linnaeus to that of Lühe (1899), all of the older writers recognizing at least two species, the larval and the adult, and many, several species under each of these. Rudolphi (1810), for instance, accepted four species of the former, "ovariis occultatis," and the same number of the latter, parasitic in the intestines of birds, "ovariis distinctis." In his Entozoorum Synopsis (1819) he reduced the number of larval species to two, but retained the same four adult forms as before. The next important move in a systematic direction was by Creplin (1839) who divided Rudolphi's *L. simplicissima* into two larval species, viz., *L. monogramma* and *L. digramma*, corresponding respectively to the previously known *L. uniserialis* and *L. interrupta* (or *alternans*), which plan was followed by Diesing (1850, 1854, and 1863) while Dujardin (1845) and Baird (1853) followed Rudolphi. Diesing (1850:581) erected a third species, *L. reptans*, to accommodate numerous forms found encysted in the muscles and connective tissues of amphibians, reptiles, birds and mammals; but as pointed out by Janicki (1906:519) several larval species were probably included under this heading. Those from avian hosts are not given above since they were found only among the

muscles and under the skin, where *L. intestinalis* has never been found in birds, so far as the available records indicate. Lühe (1910:18) did not include them in his list of hosts for the adult stage of the species.

Next in order of importance came Donnadieu's (1877) classical experiments in which, after completely reviewing the literature up to date, he conclusively proved that the form found in the body cavities of various bony fishes is the larval stage of that present in the intestines of birds. As a result of his work he combined the two forms under a new name, *Dibothrium ligula*, confusing at the same time *Schistocephalus solidus* with *Ligula intestinalis*. The life-history of the species was later studied by Riehm (1882) by feeding methods. Moniez (1881:37, 81) was the first writer to study the histology of the species, while Kiessling (1882) gave the first description of its general anatomy. As emphasized, however, by Linstow (1901a), Kiessling's work is not very specific, since he almost constantly disposed of *L. intestinalis* by saying that in it conditions were the same as in *Schistocephalus solidus*. While, apart from Donnadieu and the earlier writers, Willemoes-Suhm (1870:94) was the first to study the development of the embryo with attention to detail, Schauinsland (1885:550) enlarged upon his observations and gave a more or less complete description of the process up to the time of the escape of the ciliated larva. Niemiec (1888:2) described the nervous system, and Cohn (1898:134) pointed out its resemblance to *Sch. solidus* in this regard. Zernecke (1895) in the meantime dealt in his well known work on the finer structure of cestodes with the parenchyma and the nervous and muscular systems in particular; since then little has been done in that connection. The question of segmentation was studied by Lühe (1898). Later the same writer (1899:52) placed the species in his first classification, stating as his belief that there is only one species of Ligula, viz., *L. intestinalis* (L). The latter conclusion was also arrived at by Linstow (1901a:628), altho he attributed the specific name to Goeze; while in his latest classification Lühe (1910) maintained the same view.

Consequently, taking for granted in the absence of European material for comparison that the latter has been established as a fact for the European forms, the problem is to determine whether the same species occurs here in America. So far as the majority of specific characters are concerned, one must rely on the descriptions of Kiessling and Linstow (1901a) who seem to have been the only writers to attend to the details of the reproductive system,—and as metioned above, Kiessling's is quite inadequate in this connection. The only American reports of the species are of larval forms: *L. monogramma* by Leidy (1855:444) and *Dibothrium ligula* by Linton (1898:438), the former having also listed (1856:46) the doubtful *L. reptans*.

Lühe (1910:18) gave the dimesions of the species as 100 to 400 mm. (occasionally 1 meter) in length by from 5 to 15mm. in breadth, not distinguishing however, between the larva and the adult in this regard. Linstow (1901:629) reported a larva from *Blicca bjorkna* 200mm. long, 9 broad and 3.5 thick, adults from *Podiceps cristatus* and *Merganser merganser* 160mm. long, 4 broad and 1.5 thick. Concerning these differences he said that: "Wenn man die Geschlechts-

form aus Vögeln oft kleiner findet als die Larve aus Fischen, so mag das seinen Grund darin haben, dass die letztere sich in der Grösse ihren Wirth anpasst; die grossen Larven in grossen Fischen können aber nicht von kleineren Vögeln verschlungen werden." The largest larval specimen at hand was one from *Catostomus commersonii* which measured 425mm. in length by 15 in maximum breadth, but the largest adult from *Merganser merganser* was only 217 by 6mm. In the larva the anterior end is somewhat bluntly rounded (Fig. 1), the bothria being visible as very short grooves passing over the tip, while in the adult they are more elongated and distinct, the end of the strobila being somewhat protruded as shown in figure 2. On each surface of the larva there is a deep, median, longitudinal furrow, which however, becomes obliterated in the adult, excepting anteriorly, by the growth of the reproductive organs, the ducts of which are confined to the median line of the strobila. When these are developed the strobila is characterized dorsally by a low median ridge bounded on each side by a quite shallow groove, and ventrally by a greater thickening of the median line, not separated, however, by any grooves from the lateral regions. The whole strobila gradually tapers from a short distance behind the anterior end, where the maximum breadth is located, to the posterior end. Whereas in the larva it is quite thick, in the adult it is thin and leaf-like, the margins usually appearing wavy in alcoholic specimens, especially posteriorly. A pseudosegmentation is present in the anterior end of the strobila, but as has been known, especially since Lühe (1898) emphasized the fact, this division of the strobila into segments does not correspond with the internal division into true proglottides. Gemmill (1909:11) counted about 50 of them in the anterior third of the worm, the writer 38 or 39 for a distance of 13mm. from the tip of one adult specimen (Fig. 2) and 36 for 10mm. in another. They vary considerably in length and are often incomplete medially. From the anterior region showing external segmentation to the posterior end both larvae and adults, but particularly the latter, are crossed by very numerous irregular grooves, which give the worm its characteristic appearance apart from the general shape as contrasted, for instance, with the closely related *Schistocephalus solidus*. The smallest larva met with was one from a small specimen of *Micropterus dolomieu*, 47mm. in length. It gave the following measurements: length, 4.9mm.; maximum width, 0.54mm.; width one-third the length from the anterior end, 0.54mm., two-thirds, 0.37mm.; length of bothrial groove about 0.07mm.

The cuticula was found to have a thickness of from 5 to 15μ, compared with 16 to 18μ by Kiessling and 2.1 (!) by Linstow. It appears homogeneous in sections rather than divisible into the three layers described by the former, with some tendency, however, for the outer one-quarter to one-sixth to take the stain much less than the remainder of the tissue, which outer clearer area is often bounded by a very delicate pseudociliated layer. There is a good deal of variation not only in the thickness of the cuticula but also in its structure; and these remarks apply to the larva as well as to the adult. The subcuticula varies from 50 to 110μ in thickness, or 33 to 49μ according to Kiessling and

114μ to Linstow. Calcareous bodies in the characteristically fine parenchyma, described by Moniez and Zernecke, and given dimensions of 13 by 7.8μ by Linstow, were observed in the largest living specimens from the body-cavity of *Catostomus commersonii commersonii* to be extremely numerous, spherical to ellipsoidal in shape and to measure from 14 to 19μ in length by 12 to 17 in breadth.

The musculature has been well described histologically by Zernecke (1895); while Kiessling spoke rather briefly of its arrangement in the late larva. Later Lühe dealt with the system in general (1897a and 1898) and its relation to the nervous system (1896), and Linstow (1901a), gave a concise account of its arrangement.

The chief nerve strands are situated in transections between the lateral and median quarters of the transverse diameter of the strobila, in the median frontal plane, that is below the neighboring testes, and with a diameter of 50 to 100μ. The details of the system have been studied by Moniez (1881), Niemiec (1888), Zernecke (1895), and Cohn (1898), the latter of whom found conditions pretty much as in Schistocephalus, namely, that each chief strand has associated with it six collateral strands, arranged in three groups of two each.

The excretory system was studied by Moniez and Zernecke in considerable detail. Linstow stated that two regions accommodating numerous longitudinal vessels are present: (1) an outer, close beneath the vitelline glands, and (2) an inner, between the inner longitudinal and transverse muscles, or as Linstow figured, between the former themselves. In the material studied an outer plexus appeared close beneath, among, or most often just outside of the vitelline glands (cortical); a second and quite indistinct one among both sets of muscles, and a third, or innermost layer, as prominent as the outermost, almost in the median frontal plane of the medulla.

The sets of genitalia, beginning about 10mm. from the anterior end and very closely crowded together in the longitudinal direction, lie from 0.05 to 0.20mm. apart, 0.13 to 0.15mm. being the data given by Linstow. The openings are usually almost exactly in a transverse line; but the cirrus and uterus openings alternate irregularly from side to side, that of the vagina being constantly in the middle. This alternation of the openings is due to the similar alternation of the internal organs and evidently was the basis upon which the earlier species *L. digramma* and *L. alternans* were established. The genital cloaca is a quite irregular transverse depression, 0.18 to 0.20mm. in width and 0.02 to 0.03mm. in length, the respective measurements by Linstow being 0.106 and 0.026mm.

"The testes lie in a single row, which is only interrupted by the uterus, on the dorsal side of the medulla. . . ." They are from 20 to 40 in number in transections, ellipsoidal in shape, their greatest diameters being transverse, as indicated by the maximum width, length, and depth being, respectively, 115 to 145, 45 to 55, and 80 to 85μ. Linstow gave them as 150 to 180μ long by 88 to 156μ wide. The loosely coiled vas deferens is situated above the cirrus-sac

(Fig. 78) and roughly divided into two parts by the lateral coils of the uterus, one part being immediately above the cirrus-sac and the other close to the dorsal body wall. The duct attains a diameter of 35μ when filled with spermatozoa. Distally it expands into the very small (as compared to that of *Sch. solidus*) seminal vesicle, situated close to the dorsal wall of the cirrus-sac. The vesicle is from 65 to 100μ in length by 40 to 90μ in diameter (156 by 86μ, Linstow), oval in shape, the narrower end towards the cirrus pouch, and provided with only a comparatively feeble musculature. The wall of the structure is richly supplied both internally and externally with nuclei which are respectively those of the lining epithelium and the myoblasts, as in Schistocephalus. The epithelium is strongly ciliated. The cirrus-sac (Fig. 78) is an ovoid body, somewhat flattened dorso-ventrally and obliquely by the uterus, and alternating irregularly from right to left, always occupying the opposite side of the median line from the ovarian isthmus and the neighboring female ducts. Its wall is quite thin, while apart from the cirrus proper which occupies the distal two-thirds, the contents consist of loose parenchyma and only a few retractor muscles. The measurements of the organ in sections are: dorsoventral diameter, 185 to 215; width, 130 to 160; and length, 130 to 145μ; which are quite at variance with Linstow's diameter of 53μ of what he described as a spherical organ. Within the cirrus-sac the vas deferens is not sharply separated into ejaculatory duct and cirrus proper, altho the latter is quite distinct, closely coiled, and as much as 25μ in diameter.

The vagina opens into the common genital cloaca, if one may use that name for the depression mentioned above, in the median line and usually equidistant from the openings of the cirrus and uterus. It passes dorsally thru the cortex and the musculature with almost a straight course. Then within the medulla it turns sharply posterolaterally, in which portion of its course it has a diameter of from 15 to 30μ (5μ, Linstow). Its thin lining of cuticula, directly continuous with that of the genital depression, gradually passes into a nucleated epithelium, in which no distinct cell boundaries appear, just within the cortex. Dorsal to the ovarian isthmus it enlarges into an elongated receptaculum seminis which has a diameter of from 75 to 90μ. Linstow described a spindle-shaped terminal receptacle, 13μ in diameter, and an oocapt as follows: "dorsal von der Vereinigungsstelle der beiden Keimstocksflügel liegt der ovale, 0.088mm. lange und 0.066mm. breite Schluckapparat"; each of which, however, in comparison with that described here by the writer and for *Sch. solidus* below, seems to have been confused with the other. At least the oocapt of none of the bothriocephalids described here is relatively so large as indicated by Linstow in his measurements and in his figure, nor is the receptaculum as spindle-shaped as shown in the latter. In this connection Kiessling described a swelling of the vagina, 46μ in diameter, which contained spermatozoa. The spermiduct is so short and of such a small calibre that it is quite difficult to locate it in sections. After pursuing a horizontal course it unites with the oviduct a short distance from the oocapt (Fig. 98) much as in *Sch. solidus*. It is from 20 to 25μ in length and 6 to 12μ in diameter. The ovary is asymmetrical, as stated by Kiessling but

denied by Linstow, since it consists of a much depressed lateral wing, situated close to the ventral musculature (Fig. 78) and a more median enlarged portion which functions as the isthmus in that the oviduct arises from it. This isthmus-like region is not in the median line but about 0.25mm. from it, the whole organ alternating irregularly from right to left, constantly opposing the cirrus-sac on the other side. It varies from 0.55 to 0.64 mm. in width and has a length laterally of 0.12mm. Its unusual situation is evidently due to the closely crowded condition of the reproductive organs and the pressure exerted by the large uterus in the median line. Whereas the wing has a maximum dorsoventral diameter of about 60μ, the isthmus is about 95μ in depth and roughly ellipsoidal in shape, protruding in sections from the dorsal region of the junction of the wing (Fig. 78). Ova from the isthmus were found to be oval to spherical in shape and from 12 to 15μ in diameter (13 to 16μ, Linstow). The oocapt is directed horizontally away from the side of the isthmus and from the median line. Its diameter is from 18 to 20μ,—with which compare the dimensions of 88 by 66μ given by Linstow. The oviduct has a diameter of from 15 to 20μ. Taking a general dorsal course, after being joined by the spermiduct, it soon receives the common vitelline duct (Fig. 98) which has only a limited enlargement from a previous diameter of 10 to 20 to 30μ in the form of a vitelline reservoir, located close to the oviduct with a length of 40μ. The vitelline follicles are situated in a layer close beneath the subcuticula and unbroken, excepting in the median ventral line. The individual follicles, very irregular in shape, are 50 to 70μ in depth and 15 to 30μ in width, Linstow's measurements being 65 by 47μ and Kiessling's 6μ in the larva. Concerning the shell-gland Linstow said: "Die Schalendrüse ist ein 0.088-0.105mm. grosses Organ, das dorsal von der Mitte des einen Keimstockflügels an der entsprechenden Aussenwand der Uterus liegt; die Zellen, deren kleiner Kern sich intensiv farbt, sind 0.0039mm. gross." In the sections studied by the writer it was found to be a quite irregular structure, composed of greatly elongated club-shaped cells with necks of different lengths which unite with the oviduct in a region only about 30μ in length and situated just beyond the point of reception of the common vitelline duct (Fig. 98). These cells are so loosely arranged and their proximal attenuated portions of such a filiform nature that they are very easily overlooked, especially since they are scattered thruout the whole of the dorsoventral diameter of the medulla of the region and are interwoven among the oviduct, the receptaculum, the vitelline duct and the beginning of the uterus. They form by no means such a compact organ as Linstow's description and figure would indicate. The distal ends of the cells are about 15 by 10μ in size, while their nuclei are about 4μ in diameter. Kiessling described the shell-gland as similar to that of *Sch. solidus*, and as follows: "Die Schalendrüse besteht aus Drüsenzellen, welche an feinen Stielchen befindliche Bläschen an der Oberfläche einer Halbkugel angeordnet sind und ihre Stielchen als Radien nach dem Mittelpunkte der Kugel senden." His figures of such a compact region are likewise quite different from conditions described here. The uterus forms a mass of coils, 0.4 to 0.6mm. in diameter in the median

line, from which a straight portion passes ventrally thru the musculature and cortex to the opening which is about 20μ in diameter (35μ, Linstow). The diameter of the duct is 60μ in the median frontal plane but only half that amount as it passes thru the longitudinal muscles. The measurements of the eggs are according to Kiessling and Linstow, respectively, 49 by 34μ and 65 by 42μ: they were found by the writer to be 50 to 54 by 30 to 33μ in sections.

Our knowledge of the life-history of the species is confined chiefly to the works of Duchamp (1876), Donnadieu (1877) and Riehm (1882) who firmly established the well-known fact that the larva present in the abdominal cavities of various species of teleosts develops rapidly in the intestines of fish-eating birds. The production of eggs begins after about 36 hours, while the adults live for from three to four days only in the definitive hosts. Apart, however, from these and other closely related details which were brought out by Donnadieu by means of well conducted and controlled experiments, nothing is known, so far as the writer is aware, of the development of the oncosphere in the intermediate host up to the time when it becomes distinguishable as a small larva. The measurements of the smallest larva found in connection with this study have been given above; another slightly larger specimen was 6.1mm. in length by 1.34mm. maximum breadth.

Altho the above description shows many discrepancies between the species as here dealt with and the European form, the writer does not feel justified in separating the two specifically, especially in the absence of European material for comparison. The thickness of the cuticula, and subcuticula, the dimensions of the testes, seminal vesicle and cirrus-sac and the diameter of the vagina show the greatest differences, apart from the probable confusion by Linstow of the oocapt and receptaculum seminis, while the measurements of the eggs as here given are somewhat intermediate between those by Kiessling and Linstow. But the fact that the data given by the latter are apparently the only adequate ones for the adult and that there are not a few discrepancies between Kiessling's and Linstow's accounts restrains one from looking upon this, the American form, as new. In dealing with this question of identity it must also be remembered that not only does the species vary so much that, as pointed out above, a great deal of confusion exists in the earlier literature, but that the number of host species of the larva as well as of the adult is very large as compared to other species of bothriocephalids, hence introducing greater factors for variation. And above all the geographical distribution of the wading and diving birds harboring the mature worms is such that here in America there are many of the same species as well as the same genera that occur in Europe. As the above record of hosts indicates, the species certainly ranges widely over Europe and Northern Asia, so that it would be quite surprising if it did not occur here in North America, with the probable region of transition in Iceland and Greenland on the east and northeastern Siberia and Alaska on the west. However apart from Leidy's and Linton's records it has apparently not been reported up to the present.

The material studied by the writer consisted of the following lot of larvae: Nos. 4706 and 4708 of the collection of the United States National Museum; Ch 18a, 16.411, 16.413, 16.414, 16.419, 17.31 and 17.32 of the collection of the University of Illinois, under the care of Professor H. B. Ward; Nos. 49b, 70 to 79, 110 to 119, 361 to 370, 427 and 431c of the collection of Dr. G. R. LaRue; Nos. II, III, IV, and V from the collection of Mr. H. R. Hill; and Nos. 47, 54, 150, 158, 159, 160, 189, 190, 312, 313, 314, 317, 319, and 330 of the writer's collection; and the adults contained in Nos. La 156, 17.184, and 17.185 of the collection of the University of Illinois, respectively from the intestines of *Merganser* sp., *Podilymbus podiceps* and *Colymbus holboellii*, and No. 387g of the collection of Dr. LaRue from the intestine of *Mergus merganser*.

SCHISTOCEPHALUS Creplin 1829

Taenia (part.)	Auctorum	
Hirudo (part.)	Linnaeus	1745
Fasciola (part.)	Linnaeus	1767
Rhytis (part.)	Zeder	1800
Halysis (part.)	Zeder	1800
Bothriocephalus (part.)	Rudolphi	1808
Schistocephalus (part.)	Creplin	1829

Bothria and external segmentation developed in the larva. The tip of the scolex retractile. Segmentation complete and corresponding to the internal structure of the animal. Longitudinal and transverse muscles arranged in several alternating layers (three transverse layers enclosing two longitudinal layers).

Type (and only) species: *Schistocephalus solidus* (O. F. Müller).

SCHISTOCEPHALUS SOLIDUS (O. F. Müller 1776)

[Figs. 3, 79, 80]

LARVAL STAGE:

1734	Taenia	Frisch	1734 : 395
1745	*Hirudo depressa alba*	Linnaeus	1745 : 250
1758	*Fasciola hepatica*	Linnaeus	1758 : 648
1761	*Taenia lata*	Pallas	1761 : 410
1767	*Fasciola hepatica*	Linnaeus	1767 : 1077
1776	*Taenia solida*	Müller	1776 : 219
1780	*Taenia gasterostei*	Müller	1780 : 22
1780	*Taenia gasterostei*	Fabricius	1780 : 320
1781	*Taenia acutissima*	Pallas	1781 : 76, 78
1786	*Taenia gasterostei*	Batsch	1786 : 224
1788	*Taenia solida*	Schrank	1788 : 49
1790	*Taenia solida*	Gmelin	1790 : 3079
1790	*Taenia gasterostei*	Abildgaard	1790 : 49–58
1800	*Rhytis solida*	Zeder	1800 : 297
1810	*Bothriocephalus solidus*	Rudolphi	1810 : 57
1819	*Bothriocephalus solidus*	Rudolphi	1819 : 139, 477
1819	*Bothriocephalus solidus*	Leuckart	1819 : 46

1824	*Bothriocephalus solidus*	Nitzsch	1824 : 97
1829	*Bothriocephalus solidus*	Baer	1829 : 388
? 1863	*Schistocephalus rhynchichthydis*	Diesing	1863 : 233
1896	*Schistocephalus dimorphus*	Zschokke	1896 : 773
1896	*Schistorhynchus dimorphus*	Zschokke	1896 : 776
1898	*Schistocephalus dimorphus*	Linton	1898 : 427
1898	*Schistocephalus solidus*	Cohn	1898 : 126
1898	*Schistocephalus solidus*	Mühling	1898 : 33
1899	*Schistocephalus solidus*	Lühe	1899 : 52
1909	*Schistocephalus solidus*	Scott	1909 : 80

ADULT STAGE:

1782	*Taenia lanceolata nodosa*	Bloch	1782 : 10
1786	*Taenia lanceolata var. β*	Batsch	1786 : 167
1788	*Taenia nodularis*	Schrank	1788 : 39
1790	*Taenia lanceolata nodosa*	Gmelin	1790 : 3075
1790	*Taenia gasterostei*	Abildgaard	1790 : 49–58
1793	*Taenia lanceolata nodosa*	Rudolphi	1793 : 41
1800	*Halysis lanceolato nodosa*	Zeder	1800 : 340
1810	*Bothriocephalus nodosus*	Rudolphi	1810 : 54
1819	*Bothriocephalus nodosus*	Rudolphi	1819 : 140
1819	*Bothriocephalus nodosus*	Leuckart	1819 : 58
1824	*Bothriocephalus nodosus*	Nitzsch	1824 : 97
1829	*Schistocephalus dimorphus*	Creplin	1829 : 95
1839	*Schistocephalus dimorphus*	Creplin	1839 : 296
1845	*Schistocephalus dimorphus*	Dujardin	1845 : 622
1850	*Schistocephalus dimorphus*	Diesing	1850 : 584
1853	*Schistocephalus dimorphus*	Baird	1853 : 92
1854	*Schistocephalus dimorphus*	Diesing	1854 : 19
1858	*Schistocephalus solidus*	R. Leuckart	1858 : 129
1859	*Schistocephalus solidus*	Steenstrup	1859 : 475
1863	*Schistocephalus dimorphus*	Diesing	1863 : 232
1869	*Schistocephalus dimorphus*	Willemoes-Suhm	1869 : 469
1877	*Dibothrium ligula*	Donnadieu	1877 : 495
1881	*Schistocephalus dimorphus*	Monniez	1881 : 175
1882	*Schistocephalus dimorphus*	Kiessling	1882
1889	*Schistocephalus solidus*	Lönnberg	1889 : 40
1890	*Schistocephalus dimorphus*	Lönnberg	1890 : 18
1893	*Schistocephalus dimorphus*	Olsson	1893 : 15
1896	*Schistocephalus dimorphus*	Ariola	1896 : 280
1896	*Bothriocephalus zschokkei*	Fuhrmann	1896
1898	*Schistocephalus zschokkei*	Fuhrmann	1898 : 144
1898	*Schistocephalus solidus*	Mühling	1898 : 33
1899	*Schistocephalus nodosus*	Lühe	1899 : 52
1900	*Schistocephalus dimorphus*	Ariola	1900 : 426
1910	*Schistocephalus gasterostei*	Lühe	1910 : 19
1911	*Schistocephalus dimorphus*	Solowiow	1911 : 123

Specific diagnosis: With the characters of the genus. Medium sized worms, length 30 to 300mm., breadth 3 to 9mm. First segment or "scolex" 0.4 to 0.8mm. in length and 1 to 1.3mm. in width. Strobila ovate-lanceolate and depressed, maximum breadth anterior to the middle; hindermost segments narrower and

flatter, 0.25 to 1.0mm. in length by 1 to 3mm. in width, forming an appendage up to 10mm. in length; medium segments 0.1 to 0.5mm. long, posterior borders prominent. Shallow median groove on the ventral surface.

Cuticula 15 to 20μ in thickness; subcuticula 40 to 65μ. Layer of internal longitudinal muscles 15 to 50μ in thickness. Nerve strands 30 to 75μ in diameter. 25 to 30 excretory vessels in transections.

Genital cloaca median, shallow, with a diameter of 90μ; no hermaphroditic duct. Opening of vagina close behind that of cirrus and to one side but not so far as that of the uterus, both alternating irregularly from side to side.

Testes extend from the median genital ducts laterally to the edges of the medulla, unbroken from proglottis to proglottis, closely crowded, 240 to 480 in number for each proglottis, 85 to 100μ in depth, 40 to 65 in width and 55 to 85 in length. Vas deferens median, dorsal, closely applied to the seminal vesicle, the whole mass 0.30mm. in diameter, the duct itself 35 to 60μ. Seminal vesicle 175 by 150μ, walls 25μ in thickness. Cirrus-sac oval in shape, immediately below the seminal vesicle, 0.185 to 0.203 by 0.203 to 0.212 by 0.166 to 0.185 mm. in dimensions. No inner seminal vesicle. Cirrus proper not sharply separated from the ductus ejaculatorius; whole surrounded by numerous retractor muscles.

Vagina 45 to 60μ in diameter just within the medulla. Receptaculum seminis large, 92 to 105μ in diameter. Spermiduct unites with the oviduct close to the ventral wall of the medulla. Ovary with large wings consisting of closely arranged tubules, whole organ 0.6mm. in width, wings 0.10 in length. Ova 13μ in diameter, their nuclei 5μ. Oocapt 35 to 40μ in diameter, oviduct 25 to 30μ. Vitelline gland unbroken at margins of the proglottis, from proglottis to proglottis, and medially, excepting for small areas above and below the proximal reproductive ducts; individual follicles 55 to 90 by 18 to 26μ. Ootype 16 to 20μ in diameter. Shell-gland slightly to one side of median line. Uterus 85 to 135μ in diameter at its middle; the terminal portion directed dorsoventrally and lined with cuticula distally; opening at the bottom of a slight invagination of the ventral body wall, formed by the rupture of a pre-existing cuticular membrane.

Eggs, 38 to 65 by 22 to 38μ.

Habitat: As larvae in the body-cavities and occasionally in the stomach and intestine of bony fishes; adults in the intestines of wading and diving birds.

HOST	LOCALITY	COLLECTOR	AUTHORITY
Larval stage:			
Gasterosteus aculeatus	Greenland	Fabricius	Fabricius 1780 : 320
Cottus poecilopus	L. Storsjön, Sweden	Olsson	Olsson 1893 : 15
Cottus bairdii	Swan R., Mont.	Everman	Linton 1898 : 427
Salmo salar	Basel	Zschokke	Zschokke 1896 : 776
Phoca vitulina	Gryphswald	Rudolphi	Rudolphi 1819 : 140
Rhynchichthys gronovii	Hayti	Weinland	Diesing 1850 : 585
Gasterosteus bispinosus atkinsii	Chamcook L., New Brunswick	A. R. Cooper	Cooper (the present paper)
Uranidea formosa	Port Credit, Ontario	A. R. Cooper	" "
Gasterosteus cataphractus	R. P. Lake, St. Paul Id., Pribilof Ids., Alaska	C. E. Crompton	" "
Adult stage:			
Corvus cornix	East Prussia	Braun	Muehling 1898 : 34
Recurvirostra avocetta	.....	Schilling	Diesing 1850 : 584
Ardea stellaris	Genf	Fuhrmann	Fuhrmann 1896 : 546
Ciconia alba	East Prussia	Braun	Muehling 1898 : 34
Sterna hirundo	Gryphswald	Rudolphi	Rudolphi 1819 : 140
Colymbus septentrionalis	Firenze, Italy	Condorelli	Parona 1899 : 8
Podiceps nigricollis	Bracciano, Italy	Parona	Parona 1899 : 8
Larus ridibundus	Rossitten	Muehling	Muehling 1898 : 34
Anas glacialis	.....	Creplin	Diesing 1850 : 585
Mergus serrator	L. Storsjön, Jemtland, Sweden	Olsson	Olsson 1893 : 15
Uria troile	.....	Abildgaard	Diesing 1850 : 585
Alca torda	Leipzig	C. W. Stiles	Stiles and Hassall 1894 : 322
Totanus calidrus	Jaederen, Norway	Loennberg	Loennberg 1890 : 18
Harelda glacialis	Pillau	Muehling	Muehling 1898 : 34
Fuligula marila	Pillau	Muehling	Muehling 1898 : 34
Haematopus ostrealegus	Pillau	Muehling	Muehling 1898 : 34
Fulica atra	Portoferrajo, Id. Elba	Damiani	Parona 1899 : 7
Puffinus kuhli	Portoferrajo, Id. Elba	Damiani	Parona 1899 : 7
Urinator arcticus	.....	.....	Lühe 1910 : 19
Stercorarius parasiticus	.....	.....	Lühe 1910 : 19
Nyroca marila	.....	.....	Lühe 1910 : 19
Lophodytes cucullatus	Lincoln, Nebr.	H. B. Ward	Cooper (the present paper)

The species has also been reported in Europe from the following additional hosts:

Larval stage: *Cottus scorpio, Fulica atra, Gasterosteus pungitius, Totanus calidrus*, and *Rana esculenta*;

Adult stage: *Alca pica, Ardea cinerea, Ciconia ciconia, C. nigra, Colymbus arcticus, C. cristatus, C. glacialis, C. griseigena, C. immer, C. troile, Corvus corax, Larus argentatus, L. capistranus, L. marinus, Mergus albellus, Mergus merganser, Podiceps cristatus, P. rubricollis, Sterna arctica, S. macroura, S. minuta, S. nigra* and *Uria grylle.*

As indicated in the above synonymy this species was known for almost a century, at first as the larval form only and then as both larval and adult forms, before it was discovered that the two species recognized from the time of Bloch (1782) were one and the same. Abildgaard (1790), who called the worm *T. gasterostei*, seems to have been the first to consider the larval form found chiefly in sticklebacks to be the same as that found in fish-eating birds, since on feeding sticklebacks infected with the larvae to geese he obtained the adult form from the intestines of the latter. Yet Rudolphi (1810) did not agree with his conclusions but still considered that there were two distinct species, namely, *Bothriocephalus nodosus* (adult) and *B. solidus* (larva). And this continued until Creplin (1829) united both in one species under a new genus, *Schistocephalus dimorphus*. Diesing (1863:233) made a new species out of the *Schistocephalus* found by Weinland (1859) in the island of Hayti in *Rhynchichthys gronovii*, but later writers have considered that in all probability it was only the well known larval form of this species. Willemoes-Suhm (1869) was evidently the first to study the development of the fertilized ovum, which was later gone into more thoroughly by Schauinsland (1885:555). Donnadieu (1877), to whom all go back in their considerations of the larval development of Ligula, unfortunately fell into the error of considering Schistocephalus and Ligula to be not only the same specifically but generically. The anatomy was first studied by Moniez (1881:175), more thoroughly by Kiessling (1882), and still later by Furhmann (1896) (under *B. zschokkei* sp. nov.) and Solowiow (1911). Linton (1897:427) is the only one, apart from Weinland's record which is only a brief foot note, who has reported the species from America.

As regards the correct name of the species, it should be noted that, altho Lühe (1899:52) called the "typical and only species" of the genus *Sch. nodosus* (Rud.) and the larval stage *Sch. solidus* (O. F. Müller), he reverted in 1910 to "*Schist. gasterostei* (*Fabr.*) (=*Sch. dimorphus Crepl.*)" without, however, discussing the change. But according to the Rules of Nomenclature, Art. 27 (b), the earliest name of the larval stage must hold, so that, since Lühe himself considered this to be *Sch. solidus* (O. F. Müller), the writer makes use of the latter in the present paper.

According to Lühe (1910:19) *Sch. solidus* ranges in length from 30 to 300mm. while the maximum breadth varies from about 3 to 9mm. and is located ahead of the middle of the strobila. As shown in the table below the largest and only sexually mature specimen of the six studied by the writer was only 29mm. in length by 6mm. in breadth. The scolex (Fig. 3) is, as indicated in the above diagnosis of the subfamily, not separated from the first segment into which it runs insensibly, the whole "head" being thus triangular in shape. The bothria

are merely short median grooves which unite at the very tip not only with each other but with a frontal median groove which passes laterally into slight emarginations of the edges of the segments. While these emarginations were seen to be present in the anterior segment, gradually disappearing towards the middle of the worm, no such "flat leaflike flaps (bothria) on the lateral margins separated from each other on flat surface by a broad, shallow sulcus," as described by Linton (1898:428) and shown in his Fig. 4, Pl. XXVIII, for the first segment were met with; but the posterior border was quite entire, altho as seen in figure 3, not very prominent in the vicinity of the median line in adults as well as in larvae. The bothria of the mature specimen (H. 7 of the table below) were not present, but the region where they would otherwise be was quite smooth, only a shallow, median, frontal groove appearing. The whole strobila is ovate-lanceolate, considerably depressed and provided in the adult with a very shallow median groove on the dorsal surface (Fig. 80) which seems to be due to the slight protrusion of the median reproductive organs, chiefly the cirrus-sacs and seminal vesicles, towards the ventral surface (Fig. 79) and the consequent dragging downward of the dorsal median tissues. Concerning this matter Linton said "*S. dimorphus* is described as having in the larval state a longitudinal median furrow on each face. These specimens do not exhibit this character; neither do they have anything that can be properly called a costa dividing the two bothria." While in the specimens studied the dorsal groove was present not only in the adult but (not so well marked) in the larva, a similar ventral groove was also noticed in sections of the anterior end of one of the latter. Both grooves, however, are in either case so shallow as to be easily overlooked in alcoholic specimens; they seem to be of only secondary importance since they are apparently quite variable in their nature. While the segments in the anterior region of the strobila are very broad and comparatively thick, short, and from 0.1 to 0.5mm. in length, posteriorly the strobila is considerably smaller and flatter, especially in mature individuals. In larvae the segments are much more irregular in outline and as much as 1mm. long (0.75 in the only ripe specimen studied). The segmented condition of the strobila, in contrast with that of Ligula, is rendered more apparent by the prominent posterior borders of the anterior and middle proglottides which at the margins produce the characteristic saw-tooth effect. The following table gives the measurements of two specimens with those by Linton for comparison:

NUMBER	72	H 7	4727 U. S. N. M.
Length	17mm.	29mm.	32mm.
Maximum breadth	5.5	6	6
Length of "cauda"	1.64	10	?
Breadth of same	1.1	2-3	2.5
Length of med. segs.	0.16	0.27-0.46	0.25
Length of post. segs.	0.25-0.40	0.40-0.75	?
Length of first seg.	0.46	0.46	0.80
Breadth anteriorly	0.48	0.46	0.80
Breadth posteriorly	1.11	1.11	1.30
Length of bothrium	0.07	Absent	?
Condition	Larval	Adult	Larval

Since the essential features of the internal anatomy of this species have been worked out by the European workers, only the striking similarities and differences to and from the data given in particular by Kiessling, Fuhrmann and Solowiow will here be dealt with in support of the writer's contention, in the absence of European material for comparison, that here in America we have the same species as that found in Europe. It will be considered that, as brought out by Lühe in three controversial papers (1897, 1897b, 1899a:715) and by Cohn (1898:126, footnote), *S. zschokkei* Fuhrmann 1898 is synonymous with *S. solidus*. As a matter of fact many of the data given below will be seen to compare more favorably with those published by Fuhrmann than with those by either Kiessling or Solowiow.

According to Kiessling the cuticula is from 15 to 18μ in thickness and divisible into two layers, of which the inner and lighter is from 8 to 9μ thick, while the outer is striated or granular. Fuhrmann described a cuticula only 7μ in thickness and divided into two layers, and Solowiow gave the thickness of the "homogeneous cuticula" as 23μ. Minckert (1905a:402) said that the comidian or pseudociliated layer, present in many bothriocephalids, was quite evident in *S. nodosus* but absent on the posterior borders of the proglottides. Here the cuticula was found to be 15μ in thickness, excepting on the posterior borders where it is only 5μ, and divisible into two layers, the outer of which, a little thinner than the inner, was much lighter, granular in consistency or somewhat striated with, however, a more or less uniform external boundary. It seems to be easily separated from the inner stratum, the bounding line, in reality the innermost portion of the external layer, being in most places very light. In fact the brightness of this inner layer of the outer stratum indicates the degree of separation of the two layers in the process of sloughing off the outer, which can be easily followed in sections as described by Kiessling. This description however, applies only to the adult stage. In larvae the cuticula, altho of the same thickness, shows an outer decidedly pseudociliated layer only 4μ in depth. The subcuticula, 88.5μ in thickness in the median line according to Solowiow, was found to be from 40 to about 65μ, Kiessling having given the limits as from 29 to 38μ. While the parenchyma is as described by the

authors, very fine meshed, calcareous bodies are present in comparatively small numbers, particularly just beneath the subcuticula of the larva. Their maximum dimensions are 23 by 13μ.

The musculature has been well described by Kiessling and Fuhrmann, so that it needs only to be added that in sections of mature proglottides the outermost layer of transverse muscles as well as the outer longitudinal layer are much less numerous and hence well defined than in the larva. Whereas Kiessling gave the thickness of the external and internal longitudinal groups, which on account of their compact nature were found to be more uniform in thickness than the transverse layers, as 8 to 33 and 16 to 49μ, respectively, and Fuhrmann as 4 and 8μ, the writer found them to be 17 and 30 to 40μ.

The nervous system was first studied in detail by Niemiec (1888:9) and later more thoroughly by Colin (1898:126) who summarized its structure in the following words: "Von dem vordersten Theil, den Ganglien und der Commissur, ziehen die Hauptstränge und 12 Nebennerven rückwärts [six associated with each chief strand]. Die Nebennerven theilen sich dichotomisch in zwei Ebenen, der frontalen und radiären, ein Theil des Theilfasern rückt zwischen äussere Transversal- und Längsmuskeln, der andere bleibt weiter nach innen zu zurück, und diese Nerven treten einerseits unter einander durch Ringcommissuren, andrerseits durch radiäre Fasern mit den Hauptnerven in Verbindung." Kiessling gave the diameter of the chief nerve strands as 38μ and Solowiow as 67.9μ; here they were found to be from 30 in mature proglottides to 75μ in the anterior segments. The ganglia have a diameter of from 55 to 85μ, as compared with 77μ of Kiessling.

In transections from 25 to 30 excretory vessels appear in the medullary parenchyma with diameters ranging from 29 to 63μ. Fuhrmann gave 24 as the number, while Solowiow gave their size as 13.9 to 23.3μ. Foramina secundaria pierce the cuticula here and there, but they are not very numerous.

As indicated in the diagnosis of the subfamily the reproductive organs appear close behind the scolex. In one toto preparation of a larval specimen, number 72 of the above table, the earliest traces of their rudiments were present in the 18th proglottis, or 3.96mm. from the anterior end, while in the only mature specimen, H.7, they were in the 16th proglottis, a few eggs appearing in the uterus of the 17th. The cirrus and vagina open close together in a very shallow and sometimes quite obliterated genital cloaca having a maximum diameter of about 90μ, the vagina behind the cirrus, but only very slightly either to the right or left and not according as the uterine opening further back likewise alternates irregularly but with a greater amplitude. The three apertures form almost a right-angled triangle, as described by Kiessling; but, as was pointed out by Lühe (1899a:716) this arrangement is by no means constant but varies with the state of contraction or relaxation of the whole strobila and hence cannot be considered as specific.

The testes are arranged in a single layer in the dorsal portion of the medulla not only in the larva but also in the adult, as described by Fuhrmann, the majority of the excretory vessels being situated towards the ventral side of the

medulla. They are absolutely continuous from proglottis to proglottis. Their number in transections is from 30 to 40 (30 to 35, Kiessling) and in sagittal sections from 8 to 12 for each proglottis, thus making the total from 240 to 480 or over 300 on the average, which stands in distinct contrast with the number of about 100 given by Fuhrmann. The latter also gave their dimensions as 80 by 34μ, Kiessling as 16 to 66μ in young and 149μ in mature animals, and Solowiow as 68 to 93μ. The writer found them to be from 85 to 100μ in depth, 40 to 65μ in width and 55 to 85μ in diameter. They are, as indicated by their numbers, very closely crowded together in the proglottis. The vas deferens forms a compact mass of coils situated in the median line dorsally and slightly posterior to the vesicula seminalis to which it is closely applied as a sort of cap. While the diameter of the whole organ is about 0.3mm. that of the duct itself varies from 35 to 60μ when distended with spermatozoa. Kiessling gave its diameter as 38μ and Solowiow as 16.3μ. The large thick-walled seminal vesicle (Fig. 80) situated immediately above the cirrus-sac was found to have a maximum depth of 175μ and transverse diameter of 150μ, as compared with the 92μ of Kiessling and the 80μ of Fuhrmann. Its walls are very muscular, about 25μ in greatest thickness, and covered both internally and externally with numerous nuclei which are respectively epithelial and parenchymatous or myoblastic in their nature. Within the cirrus-sac the vas deferens is much coiled but not enlarged to form any secondary vesicle nor sharply separated into an ejaculatory duct and cirrus proper. The sac itself is oval in shape, the ventral end being the smaller, and the proximal end somewhat invaginated by the seminal vesicle. Its size is shown in the following table:

	KIESSLING	FUHRMANN	SOLOWIOW	THE WRITER
Depth	0.347mm.	0.25mm.	0.204mm.	0.185 to 0.203mm.
Width	0.192mm.	0.12mm.	0.174mm.	0.203 to 0.212mm.
Length	.....	.....	.....	0.166 to 0.185mm.

Its wall about equal in thickness to that of the seminal vesicle is, however, more open in texture, the myoblastic nuclei of the obliquely arranged muscle fibres being scattered thruout its diameter (Fig. 80). It is furthermore, not sharply separated either externally or internally from the surrounding parenchyma nor the numerous stout retractor muscles of the cirrus, respectively. The latter, in fact, constitute practically the whole of the contents of the sac apart from the duct itself. The only protruded cirrus seen had a length of 70μ, as compared with the 0.3945mm. given by Solowiow.

The vagina, the opening of which is usually situated about 50μ from that of the cirrus at the bottom of the shallow genital cloaca above mentioned, has a diameter of from 45 to 60μ at the first bend in its course within the medullary parenchyma. Soon after it enters the latter it becomes thin-walled, as pointed out by Fuhrmann, owing to the thinning out of the cuticula and the substitution of the proximal nucleated epithelium for the same, altho more peripherally much flattened nuclei are to be seen beneath the cuticula and crowded close to the basement membrane. In other words the gradual replacement from

within outwards of the cuticula for the original epithelium may be followed very easily in the walls of the vagina. The duct gradually enlarges to form a much elongated receptaculum seminis (Fig. 79) with a diameter of 92 to 104μ (9 to 21μ, according to Kiessling!) and sharply separated from the spermiduct, which, however, was not found to unite with the oviduct close to the dorsal transverse musculature as stated by Fuhrmann, but close to the ventral wall of the medulla. The ovary consists of two large wings (Fig. 79), composed of closely crowded tubules, lying immediately upon the ventral transverse muscles and united by a much smaller isthmus, the whole having a width of 0.64mm. as compared with the 0.28mm. of Solowiow. The average length and depth of the wings are, respectively, 105 and 90μ. Ova from the isthmus and more median portions of the wings of the ovary have a diameter of 13μ while their nuclei are 5μ. The respective measurements by Kiessling and Solowiow are 9 and 6μ and 13.9 to 23.3μ and 1.5 to 2μ. Fuhrmann stated that one of the most important differences between his *Sch. zschokkei* and *Sch. solidus* was the presence in the former of an oocapt, but Lühe (1899a:717) claimed that this structure was in all probability overlooked by Kiessling. It arises from the posterior aspect of the isthmus almost in the median line with a diameter of from 35 to 40μ. The oviduct, according to Kiessling has a diameter of 13, or to Solowiow of 27μ; here it was found to be from 25 to 30μ between the entrance of the vagina and that of the common vitelline duct, which two points are close together as in *L. intestinalis*. The common vitelline duct enlarges some little distance from its opening into the oviduct to form a vitelline reservoir having a diameter of 30μ (23μ, Kiessling). The vitelline follicles are extremely numerous and closely crowded together in a layer with a maximum thickness of 85μ, situated between the inner longitudinal and middle transverse muscles (Fig. 79). They are continuous at the margins of the proglottis as they are from joint to joint, and are broken only in limited elliptical areas above and below the reproductive ducts in the median line, as stated by Fuhrmann. The dimensions of the individual follicles are from 58 to 87 by 18 to 26μ, the larger dimensions being the dorsoventral diameters,—56 to 107 by 56μ, according to Kiessling, and 18 by 27μ after Solowiow. Just beyond the entrance of the common vitelline duct the oviduct enlarges to form the ootype with a diameter of 16μ (20μ, Kiessling) which is surrounded by the shell-gland, situated just above the median frontal plane and somewhat lateral. Thruout its course the oviduct is lined with an epithelium in which prominent nuclei but no distinct cell boundaries appear and from which numerous cilia protrude into the lumen. In the ootype these cilia are much more noticeable. From the ootype the oviduct passes ventrally with a few coils, then across the median line close above the receptaculum seminis as the beginning of the uterus. The latter gradually enlarges as it passes forward across the median line several times, until at about the middle of its course it has a diameter of 85 to 135μ. As regards the terminal portion of the tube it was found that, as Fuhrmann observed: "Der Endtheil der Uterus verengert sich und verläuft von der Dorsalfläche [the median frontal plane in which the last trans-

verse coil is situated] direkt ventral, um regelmässig abwechselnd links oder rechts neben der Vagina auszumünden."

Sections show that the actual opening is formed by the rupture of the bottom of a cup-like invagination of the cuticula from the ventral surface, which meets the end of the duct with a diameter of from 25 to 40μ. As Fuhrmann stated, "Dieser Ausführgang der Uterus ist von der Stelle an, wo er ins Rindenparenchym tritt, wie die Vagina und der Cirrusbeutel, von zahlreichen Parenchymmuskeln umhüllt und von einer der Körpercuticula ähnlichen Membran ausgekleidet;" but the cuticula seems to appear as such only near the opening, since only half-way back along this dorsoventral limb of the organ flattened nuclei are distinctly seen. In other words the flattened epithelium of the uterus, which, showing only a few scattered nuclei, was described by Kiessling as a "fine, structureless but elastic membrane," passes insensibly into the cuticula near the opening, no distinct line of junction between the two being discernible. This latter statement is likewise applicable to the similar structure of the vagina.

The dimensions of the ellipsoidal eggs in the sections of the uterus were found to be 62 to 65 by 33 to 36μ. Kiessling gave them as 49 by 37μ and Fuhrmann as 70 by 29μ. In discussing the latter, however, Lühe (1899a:718) remarked that not only did he find variations from 38 by 22 to 56 by 38μ in the size of the eggs in material of *B. zschokkei* sent to him by Fuhrmann, but that in general even greater variations than these are to be found in other species according to the various writers.

Our knowledge of the life-history of this species dates from the time of Abildgaard (1790) who, as mentioned above, was the first to experiment with the larval individuals found in fishes. Creplin (1829) united the two forms which were considered to be two separate species into one species, evidently on the basis of the previous work, especially Abildgaard's (cf. Donnadieu, 1877:340), while Donnadieu in his elaborate experiments on the life history of Ligula unfortunately did not differentiate between it and Schistocephalus. The development of the fertilized embryo into the oncosphere was first studied by Willemoes-Suhm (1869) and later more in detail by Schauinsland (1885:555), since when nothing of special importance has been added, so far as the writer is aware. Hence up to the present nothing is known about the development of the oncosphere into the larva in the intermediate host, as is indeed the case with most of the bothriocephalids.

As regards the identity of the material studied with the European species it will be seen from the above comparisons that, while there are many discrepancies among the data given by Kiessling, Fuhrmann and Solowiow, those by the latter departing the farthest in many respects, the resemblances so outweigh the differences as to make the erection of a new species unjustifiable. The thickness of the cuticula, the diameter of the excretory vessels, the dimensions of the seminal vesicle, the ovary and the eggs, which constitute the majority of the differences, might easily be explained by differences in age of the material studied. But the number of testes (100) as given by Fuhrmann

can scarcely be reconciled with that given here (300+), altho his dimensions of the organs agree with these perhaps better than do those by Kiessling or Solowiow. On the other hand there is another factor which may be in the long run more important than a comparison of the details of the anatomy of this evidently highly variable species, namely, the geographical distribution of the hosts. Altho little emphasis can be placed on Fabricius' finding *T. gasterostei* in the type larval host as long ago as 1780 in Greenland, it must be remembered that here in America there are, as in the case of *L. intestinalis*, a number of not only the same genera but also of the same species of the larval as well as of the adult hosts as in Europe. From this alone one would be justified in expecting to find the same species of Schistocephalus here, especially since it infests such a number of different host species. But it is a very surprising fact that apart from Linton's report of the larva from Montana evidently no one has up to the present found the form in any of the numerous fish-eating birds of the continent.

This evident infrequent occurrence of the species is illustrated by the fact that the material used for the present study consisted of only five lots: Nos. 61b and 72 from the body cavities of *Uranidea formosa*, taken from the stomach of *Lota maculosa*, and 190 from the coelom of *Gasterosteus bispinosus atkinsii*, of the writer's collection; one lot from *Gasterosteus cataphractus* from Alaska; and No. 17.192 of the collection of the University of Illinois from the intestine of *Lophodytes cucullatus*, the only mature specimen available.

HAPLOBOTHRIINAE Cooper 1917

Strobila formed by the subdivision of the segments of a primary strobila. Scolex of the latter a cylindrical, somewhat club-shaped organ bearing four eversible proboscides similar in structure to those of the Trypanorhyncha; scolex of the secondary (definitive) strobila merely the slightly modified foremost segment, provided with shallow dorsoventral depressions analogous to the bothria of other bothriocephalids. An elongated neck may be said to be present in the primary strobila. Segmentation of the primary strobila resulting in the formation some distance behind the scolex of a comparatively small number of long, narrow segments which in turn subdivide anteriorly to form the segments of the secondary strobila. Segmentation in the latter thus beginning immediately behind the secondary scolex, but complete in its anterior region only. Genital organs simple in each proglottis. Genital openings surficial, ventral and median as in the Diphyllobothriinae. Ovary and shell-gland median, respectively ventral and dorsal. Vitelline follicles in the medullary parenchyma, as are the testes, both within the nerve trunks. Testes separated into two lateral fields by the median excretory vessel and the genital organs in the median line. Vas deferens enlarged to form a large non-muscular seminal vesicle before entering the cirrus-sac. Cirrus armed with minute spines. Receptaculum seminis medium sized, sharply separated from the spermiduct. Uterus divided into a much coiled, proximal uterine duct and a large uterus-sac, as in the Ptychobothriidae.

Type genus: Haplobothrium Cooper.

Altho as yet comparatively little is known about the life-histories of the bothriocephalids, it has been shown that the definitive scolex and strobila develop directly from the larval stage, known as the plerocercoid, which is present in the intermediate host. This is certainly the case with Ligula, Schistocephalus, *Diphyllobothrium latum*, *Cyathocephalus truncatus* and Triaenophorus. As a matter of fact in all of these the scolex is more or less well formed before the larva reaches the final host; and after that the plerocercoid continues to grow and soon shows the beginnings of segmentation which mark the young strobila. Consequently the writer feels that what in the present paper is called the primary strobila of Haplobothrium must be looked upon as the true strobila, homologous to the young strobila of other bothriocephalids. This is contended in spite of the fact that what was formerly considered (Cooper, 1914, 1914a) to be the strobila is quite similar, apart from the absence of external segmentation in its posterior region, to that of other members of the order. Even tho it is provided with a very aberrant scolex region—and the scolex is no more sharply set off from the rest of the larva in other species, such as *D. latum*—the young unsegmented primary strobila may be considered to be a typical plerocercoid.

The nervous system is typical in that it consists of two chief strands united anteriorly by a commissure. The relatively large size of the latter, however,

seems to be due to the proximity of the highly specialized proboscides to which it sends large branches. The excretory system is likewise built on the typical plan, the posterior connections with the exterior being, in fact, quite like those of *B. scorpii*. On the other hand, the terminations of the nervous and excretory systems in the secondary strobila, both anteriorly and posteriorly support the view that the latter is not homologous with the strobila of other bothriocephalids. What was formerly described as the ring commissure must now be considered as merely a secondary formation due to the fusion of the severed ends of the chief strands; which statement is also applicable to the terminal vesicle of the excretory system. And this, in spite of the fact that the secondary scolex is quite similar to the true scolex of other forms in that it is supplied with two sets of muscles which are not found in the foremost segments, but are peculiar to the scolex.

Since there is considerable evidence in the literature on cestodes to show that the prominent posterior borders of the foremost segments of many species are developed as accessory organs of attachment or for locomotion (cf. Spengel, 1905:281), the question might well be raised whether external segmentation in Haplobothrium is palingenetic or cenogenetic in its nature, particularly since it is confined to the anterior region of the secondary strobila. The facts that no such appendages are present in the primary strobila and that the posterior end of the secondary one is not segmented, apart from the consecutive sets of genitalia, would seem to point to the original condition being one in which external segmentation was absent as in Ligula or Triaenophorus. Since, however, in the middle region of the secondary strobila there is an actual correspondence between the external and the internal segments, it is quite probable that the external segmentation is much older than might at first appear, while the ligulate condition of the posterior end may have developed secondarily. It is well to remember, too, in this connection that according to Lühe (1898:285) Ligula has descended from fully segmented bothriocephalids.

The subfamily, which up to the present contains only one genus and one species, bears a general resemblance to the Diphyllobothriinae. It differs from the latter, however, in that the genital organs are simple in each proglottis; the vitelline follicles are medullary; the testes are within (i.e., medial to) the nerve trunks; the seminal vesicle is not strongly muscular; the cirrus is armed with minute spines; the receptaculum seminis is medium sized; while the uterus is divided into a uterine duct and uterus-sac as in the Ptychobothriidae.

HAPLOBOTHRIUM Cooper 1914, e. p.

Haplobothrium Cooper 1914:1-2, 1914a:115

Borders of the terminal disc of the secondary scolex and of the posterior auricular appendages of both scolex and anterior segments provided with minute spines which disappear with the appendages farther back. Nervous system consists of two chief strands situated in the medullary parenchyma outside of the vitelline follicles, uniting in the anterior end of the secondary strobila to form a secondary nerve ring, and eight collateral strands, four arranged around

each main tract, the latter in the jointed portion of the strobila only, but in the true scolex to form an irregular transverse commissure situated among the proboscides. Excretory system composed of one large median and slightly dorsal vessel and two smaller lateral and ventral, all uniting in the secondary scolex behind the nerve ring to form a vesicle. No genital cloaca; opening of vagina close behind that of cirrus, towards the anterior end of the proglottis, that of the uterus much farther back. Sphincter vaginae present. Vitelline glands in numerous follicles arranged cylindrically around the testes, both continuous from proglottis to proglottis, leaving clear areas opposite the central genital ducts; large vitelline reservoir. Vas deferens provided with a sperm-reservoir at its posterior end near the middle of the proglottis; whole of the course of the duct dorsal to the uterus-sac. Uterus-sac when gravid occupies the whole of the middle of the proglottis.

Type and only species: *H. globuliforme* Cooper.

The genus is here emended owing to the elevarion to subfamily rank of a number of the characters given in my original generic description.

HAPLOBOTHRIUM GLOBULIFORME Cooper 1914

[Figures 9, 10, 43, 44, 65-67]

1914 *Haplobothrium globuliforme* Cooper 1914:2, 1914a:115

Specific diagnosis: With the characters of the genus. Small worms, primary strobila up to 70mm. in length, secondary to 110mm., with respective maximum breadths of 0.3 and 0.6mm. Primary scolex 0.35mm. in diameter, indefinite in length, bulbs 0.40 to 0.45 by 0.06 to 0.07mm.; secondary scolex, 0.4 to 0.5 by 0.25 to 0.4mm. Auricular appendages disappear at about the 25th segment in normal secondary strobilas. Foremost secondary segments tetragonal, middle and posterior much elongated and considerably depressed.

Cuticula 3 to 4μ in thickness, subcuticula 25μ. Chief nerve strands 18μ in diameter, narrowing intersegmentally. Terminal excretory vesicle 20 to 40μ in diameter.

Genital organs begin at about the 15th proglottis. Opening of cirrus and vagina 0.02 to 0.07mm. apart.

Testes spherical to ellipsoidal in shape, 70 to 115μ in maximum length; about 80 in each segment. Vas deferens median, elongated, only slightly coiled, 10 to 55μ in diameter. Vesicula seminalis broadly spindle-shaped, 140 by 90μ. Cirrus 20 to 30μ in diameter; cirrus-sac, 0.16 to 0.21 by 0.14 to 0.16 by 0.18 to 0.20mm.

Vagina 20 to 30μ in diameter at its opening, 56μ in its enlarged distal portion. Receptaculum seminis 30 to 45μ in diameter, spermiduct 5 to 10μ and very muscular. Ovary hippocrepiform, the limbs directed posteriorly and often fused with each other, the isthmus narrow. Ova from latter 10 to 12μ in diameter, their nuclei, 7μ. Oocapt 15 to 25μ in diameter, oviduct 8 to 15μ.

Two vitelline ducts, each 6μ in diameter; vitelline reservoir 25 to 55μ; follicles spherical or ellipsoidal in shape, 8 to 50μ in diameter, very numerous and closely crowded. Ootype 20μ in diameter; shell-gland irregular in shape, poorly developed. Uterine duct enlarged proximally with few coils, smaller distally and more coiled, median, 25 to 55μ in diameter; uterus-sac elongated, filling most of the medulla when gravid; uterus opening a small median elongated slit, situated near the posterior end of the sac.

Eggs, 60 to 70 by 40 to 43μ.

Habitat: In the intestine of *Amia calva* L.

HOST	LOCALITY	COLLECTOR	AUTHORITY
Amia calva L. (type host)	Go-Home Bay, Muskoka, Ontario	A. R. Cooper	Cooper 1914a : 81
" "	Havana, Illinois	H. B. Ward	Cooper (the present paper)
" "	Fairport, Iowa	"	"

Type specimen: No 33.1 in the writer's collection.

Co-types: Nos. 33.2 and 33.3 of the same, in the collection of the University of Illinois

In a preliminary paper on the systematic position of this species the writer (1914:1) described the scolex as ". . . unarmed, although the edges of the terminal disc and auricular appendages of both scolex and anterior proglottides are provided with very minute spines. Bothria, two shallow depressions on the dorsal and ventral surfaces, very simple in structure," and in the detailed description which followed (1914a) the organ was dealt with as follows (p. 82): "The scolex is quite small, simple externally, and with the unaided eye can scarcely be distinguished from the first joints. It is shaped roughly like a rectangular solid, hollowed out laterally to form simple depressions and dorso-ventrally the shallow bothria or organs of attachment. The summit is somewhat prolonged as a low pyramidally-shaped disc, quite comparable to that ("Scheitelplatte") found in the members of the subfamily Triaenophorinae Lühe 1899. . . . The opposite end of the scolex is modified to form two pairs of auricular appendages closely resembling internally as well as externally those of the foremost joints." Furthermore, in both papers it was emphasized that the scolex differs little in structure, apart from the nervous and excretory systems, from the first segments, and that the simple bothria seem of little functional importance as compared to those of other species while the auricular appendages of both scolex and foremost joints with their borders of minute cuticular spines probably act as accessory organs of attachment. Since then the latter view has been rendered still more highly probable, altho as yet no observations have been made on the living worms in their relation to the wall of the host's intestine, by the discovery that the so-called scolex (Figs. 9 and 10) is not in reality the scolex but only a slightly modified anterior segment.

The true scolex is something quite different from anything present in the whole order so far as the writer is aware. As shown in figures 43, and 44, it con-

sists of the slightly enlarged anterior end of the original plerocercoid or larva from which protrude four proboscides, the whole somewhat resembling a hydra and at once reminding one of the Trypanorhyncha. As will be presently seen the latter comparison is a very apt one. Each proboscis consists of a permanently protruded base or stump, as indicated in figure 43, about 85μ in length and 45 to 55μ in diameter, and an eversible proboscis proper having about the same diameter. The former is somewhat conical in shape and thickly set with minute, posteriorly directed cuticular spines which pass on to the neighboring portions of the scolex for a short distance. The whole forms at first sight a continuous tentacle gradually diminishing in size to the pointed end. These tentacles attain a length of 0.35mm., including the base, when fully evaginated, and are directed almost at right angles to the longitudinal axis of the larva, their bases being, however, turned slightly forward (Fig. 43). Within the scolex the tentacles are accommodated in elongated cylindrical muscular sacs which are quite comparable in structure to the bulbs of the Trypanorhyncha. These (the sacs) lie freely in the loose parenchymatous tissue in the diagonal diameters of the region. When the proboscides are invaginated, they have a length of 0.45mm. with a diameter of 0.07, or 0.40 by 0.06 when the tentacles are protruded. The walls of the bulb (Fig. 67) are composed of two thick layers of muscles, an outer longitudinal or somewhat oblique—much the heavier of the two—and an inner circular, and a cuticula-like lining, on the inner border of which in transections numerous flattened nuclei appear. The walls are attached to the edge of the stump, and these layers have the same relative arrangement as that of the cuticula and cuticular muscles on the outside of the body, only being in the reverse order. Continuous also with the edge of the stumps are the walls of the proboscis proper, which consist of a thin external layer of cuticula and only feeble cuticular muscles. Attached to the wall internally thruout its course are the retractor muscles of the proboscis which pass backward and become attached to the posterior end of the bulb. These can be seen best in longitudinal sections where the proboscis is retracted, for then they are closely crowded and much thicker, and their attachment to the inner end of the proboscis is nicely shown. In the retracted condition the latter is, of course, hollow, the narrow cavity often triradiate in transection (Fig. 67) being easily followed into the bulb for about one-third of its length. Closely applied to the cuticula of the tip of the proboscis appear in some cases gland-like cells taking the counterstain quite like those behind the bulbs to be described below. They are shown in figure 67. Apart from the structures already described, the contents of the bulbs and consequently of the proboscides to a certain extent, consist of a small amount of loose parenchymatous tissue and what is evidently a good deal of nervous tissue coming into the posterior end of the organ.

Evagination of the proboscides is evidently brought about by the contraction of the muscles in the walls of the bulbs, but the body wall in the vicinity of the latter probably greatly assists since its musculature is well developed. Some distance behind the posterior ends of the bulbs the latter consists of a

ring-like layer of loosely arranged main longitudinal fibres occupying the middle one-third of the radius of the nearly circular cross-section; no transverse fibres; but comparatively strong cuticular muscles, of which the inner longitudinal layer is the more pronounced. Farther forward this main longitudinal group gradually gives off small fibres towards the cuticula as they themselves diminish in number and size, until at the level of the hinder ends of the bulbs only a few of the latter fibres are left just beneath the subcuticula. An outer series at the same time forms a compact layer situated close to the longitudinal cuticular fibres (and hence outside of the subcuticular nuclei) but separated from them by a thin stratum of circular fibres. And this continues to the tip of the scolex, most of the remaining inner longitudinal muscles being located at the ends of the transverse and dorsoventral diameters of the transection. In the region of the bulbs the body wall is thus quite muscular, and in all probability assists the bulbs in evaginating the proboscides by compressing the whole of the parenchyma surrounding them. Between the bulbs and right beneath the tip of the scolex a few transverse and sagittal fibres are to be found, while just beneath the bases of the stumps of the proboscides the outer longitudinal muscles unite with the longitudinal cuticular fibres to form ∩-shaped loops surrounding the diagonal quadrants of the scolex which accommodate the bulbs. These loops are evidently for the control of the direction of the proboscis stumps.

Owing to the fact that, as originally stated by the writer (1914a:96), "there is a more or less definite point in the strobila, at or about the 15th proglottis, ahead of which the genital organs do not seem to develop and behind which in older strobilas they appear very quickly," and the further fact that not only do the auricular appendages of the posterior ends of the proglottides disappear at about the same place constantly, namely, at about the 23rd or 24th segment, it might seem that the (secondary) strobila is composed of a more or less definite and predetermined number of segments. But this is not the case, as will be seen presently when the method of formation of new proglottides is described. As a matter of fact segmentation in this species is carried on after an entirely novel plan, involving the formation of not only new segments but whole chains of them or, indeed, whole strobilas from the original larval or primary strobila as it is here called.

The original larva which resembles the bothriocephalid plerocercoid, excepting for the peculiar scolex, gradually elongates with growth, until between a length of 4 or 5mm. the first traces of segmentation appear in the hinder ends of cleared specimens as feeble aggregations of nuclei forming faint dark lines at regular intervals. In one specimen 4.8mm. in length five intervals were made out, the second last of which was 0.37mm. in length by 0.20mm. in diameter, while the last one was slightly larger and rounded posteriorly. These primary segments elongate with the growth of the strobila, and the constrictions between them gradually deepen as their anterior and posterior ends enlarge slightly, the former relatively faster than the latter. When a total length of strobila of about 10mm. is reached, the hindermost segment,

itself now about 1.5mm. in length, begins to show faint transverse lines in its anterior end, decreasing in intensity from ahead backwards. These are the earliest traces of the divisions of the primary segments into the secondary segments which will become the definitive joints of the anterior ends of the adult strobilas. In other words the original primary larva, plerocercoid or strobila, divides up into secondary strobilas which eventually separate from each other and grow into the adult chains as described above for the species. But long before separation takes place the entire development of the anterior segments with their characteristic posterior auricular appendages and the formation in particular of the first segment can be followed in these primary strobilas (Fig. 44). Whereas originally (Cooper 1914a:82, Figs. 5 and 6, Pl. V) attention was drawn to young scolices with only 5 to 8 segments, it was found in connection with the present study that the latter number, about 8 in external view or 16 or 17 in cleared specimens, is in reality that developed by the secondary strobilas before detachment from the original chain. The smaller strobilas are now looked upon as having been prematurely and accidentally separated from the posterior end of the primary strobila. The attachment soon becomes very slight, owing to the rapid deepening of the constriction ahead of the first segment, so that some time before the auricular appendages of the latter are fully delimited posteriorly very little manipulation of even alcoholic specimens, let alone cleared ones, suffices to break up the chain. However, there was found intact in the material at hand one primary strobila 88mm. in length, showing twenty secondary strobilas, including the undifferentiated anterior segments from which they are developed. Furthermore, the last two of these, 10.4 and 11.5mm. in length, showed in their posterior unsegmented portions the earliest traces of the rudiments of the reproductive organs. As has been already intimated the anterior segments form within the secondary or definitive strobilas by a gradual demarcation from head backwards, first internally in the parenchyma—actually as transverse layers of nuclei (Fig. 44) which will eventually form the posterior auricular appendages —and then externally as shown in the figure.

A continued search for evidence in connection with the question of whether or not there is in the secondary strobila a definite number of segments (external and genital combined) brought out further interesting facts. The number was counted in several young strobilas, evidently not long separated from the primary strobila, with the following results in the case of four typical specimens: (1) Length, 19mm., number of segments, 45; (2) 27mm., 29 or 30; (3) 26.5mm., 30 (the posterior ones here ripe as in the next specimen); (4) 41mm., 32 segments. It would seem from these data that there is a more or less definite number of segments, which might be considered to be about 30. But in No. 3 segments 9, 10 and 11 were not only much elongated but further subdivided anteriorly; while in No. 4 similar conditions were present in segments 10, 11 and 12, excepting that in the case of the eleventh the aggregations of nuclei indicating the subdivisions were in the posterior end. Similar elongated segments in still other strobilas show this condition in their middle regions.

Thus there is a tertiary subdivision of the secondary segments, which must, however, be considered as by no means as regular as the secondary subdivision of the original primary segments. These facts explain the aberrant nature of the strobila in this region, noted formerly by the writer, and the presence in material of chains showing anteriorly very young segments similar to those formed in the oldest attached secondary strobilas but posteriorly much older segments with well-developed auricles and farther back the typical mature proglottides of the ordinary strobila. Consequently it is probable that there is not a definite number of segments formed, but that further, irregular and evidently indefinite subdivision, resulting in the formation of an inconstant number, takes place chiefly in the middle portion of the anterior segmented region of what now must obviously be called the secondary strobila.

In the light of this method of segmentation certain facts in connection with the nervous and excretory systems that were previously considered to be very unique, to say the least, will now be explicable. In primary strobilas, even those that are youngest, the excretory system consists, as in the adult, of a larger median vessel and two lateral vessels which run backward and unite in the posterior end to form a plexus from which very many small vessels pass to the exterior by prominent foramina secundaria piercing the cuticula, much as described by Fraipont (1881:11, Fig. 7, Pl. II) for *Bothriocephalus scorpii*. In the youngest larva I have been able to find only the median vessel, which becomes greatly reduced in diameter about twice the length of the bulbs from the anterior end is present in the scolex. It forms a simple plexus among the bulbs anteriorly. In primary strobilas, however, in which segmentation has gotten well under way, all three vessels are quite prominent. They pass close to each other as well as to the chief nerve strands, when they traverse the constrictions between the developing secondary strobilas, where the median vessel is somewhat enlarged. As they near the anterior end of the worm they give off numerous branches of their own calibre, and when they meet the large ganglionic mass described below, diverge as four vessels (two on each side) and continue lateral to the bulbs to the tip of the scolex. Here after forming an open plexus among the anterior ends of the former, they unite in a single median frontal loop. As the constrictions between the secondary strobilas deepen all three vessels likewise become gradually constricted until eventually they are cut off, and the adult conditions are subsequently developed by the simple process of the turning in of both severed ends. And since in these younger forms the median vessel is considerably enlarged at the region of constriction, it remains thus in the hinder end of the adult strobila as well as in the first segment—as described and figured elsewhere by the writer (1914a:93, Figs. 12, 37)—while in the latter it is joined by the lateral vessels to form the characteristic terminal vesicle.

The nervous system of the primary strobila consists of two chief strands passing thruout the segments, a quite irregular commissure connecting them anteriorly, and a very large ganglionic mass situated some distance posterior to the proboscis bulbs. The chief nerve strands, which are quite indistinct

at different levels but constantly located in the median frontal plane, diverge as they meet the ganglionic mass in passing forward, and consequently opposite the bulbs come to lie close to the subcuticula laterally (Fig. 65). About 0.2mm. from the tip of the scolex they are united by a very irregular but comparatively large transverse commissure, from which large trunks pass to the neighboring bulbs both forward and backward. This commissure has a length or longitudinal diameter of about 0.10mm., while its maximum depth between the lateral pairs of proboscides is about 40μ. It gives off large branches anteriad to the lateral walls of the bulbs and caudad to the central walls. In the latter case a large branch leaves the median portion of the commissure, which is incidentally freely pierced with excretory vessels on each surface, and shortly divides into two, each supplying the central walls of one of the frontal pairs of bulbs (Fig. 65). The anterior branches likewise arise in a common trunk on each side, which is in reality the continuation of the lateral ganglionic enlargements of the commissure, but they supply the outside walls of the lateral pairs of bulbs. Imbedded in the commissure are numerous nuclei which, on account of their larger size than the neighboring parenchymatous nuclei, are probably ganglionic or nervous in their nature. Just behind the posterior ends of the bulbs and extending from 0.8 to 0.9mm. farther backwards (Fig. 43) there is a large mass of large nucleated cells which in transverse sections (Fig. 66) is seen to occupy the whole of the medulla (and about the whole of the section) excepting for the excretory vessels. These cells are roughly spherical in shape and have a maximum diameter of 25μ, their nuclei being 5μ. On account of their finely granular consistency and their taking the counterstain quite like the anterior nervous commissure they were interpreted as being ganglionic cells. And this view was supported on closer study by the discovery that they are not only united laterally with the chief nerve strands (Fig. 66), which can scarcely be distinguished from them at various levels, but with each other thru a complicated plexus of fine longitudinal strands which pass forward towards the bulbs and form around their bases an almost solid mass of fibrils (Fig. 43). From this mass large strands from 10 to 15μ in diameter pass into the bases of the bulbs, one for each, and are distributed among the retractor muscles of the proboscis which they evidently supply. In the youngest primary strobilas but not in the older ones, this mass of fibrils at the bases of the bulbs evidently connects forward by a few strands with the commissure.

Just as the definitive form of the anterior and posterior ends of the excretory system is explained by the separation of the secondary strobilas and the subsequent growing over of the ends, so is that of the nervous system, particularly anteriorly. As was noted by the writer (1914a) in connection with the preparation of the original description of this species and shown in figure 11, the nerve-ring is drawn out anteriorly into a point which is directly opposite a small conical pit in the tip of the scolex. This fact, as well as the relatively small size of the nerve-ring, is explained by the contraction of the free end of the "scolex" after separation and the growing together of the ends of the nerve strands to form the ring. The close association of the nerve-ring

and the terminal excretory vesicle is also comprehensible in the light of this method of development, for, since the nerve strands are situated close outside the lateral excretory vessels at the constrictions, they simply turn in towards the median line and unite immediately ahead of the junction of the latter with the median vessel.

As will be gathered from the foregoing description there is a most remarkable resemblance between the scolex of *H. globuliforme* and that of the Trypanorhyncha not only in the structure of the proboscides but also in the presence of the large mass of ganglionic cells associated with them posteriorly. Each proboscis consists of three parts: (1) a hollow tentacle, capable of evagination, (2) a short permanently protruded stump, armed with thickly set minute, cuticular spines, and (3) a comparatively elongated bulb. Of these parts (1) and (3) may be compared respectively with the proboscis and the bulb of Tetrarhynchus or Rhynchobothrius. The proboscis, altho not provided with any kind of armature, is nevertheless supplied with a group of well developed retractor muscles which are evidently analogous at least to the single retractor muscle of the Trypanorhyncha. The bulb is not only provided with a musculature arranged so as to diminish on contraction the volume of the organ, but is also lined with an epithelium-like layer comparable to that of the members of the latter group. But since the bulb extends to the point of exit of the proboscis, there is no part corresponding strictly to the proboscis-sheath of Tetrarhynchus altho the stump would at first sight seem to be such. Furthermore, the cells forming the large mass behind the bulbs in Haplobothrium which are here interpreted as ganglionic cells, bear not a little resemblance to those described by Braun (1896:1294) after Pintner (1880), Lang (1881) and Niemiec (1888) as associated with the bulbs of *Tetrarhynchus longicollis* (v. Ben.) (=*Dibothriorhynchus ruficollis* Monticelli) and considered by some to be ganglionic cells and by others myoblasts. The distribution of the large nerve trunks arising from the nerve commissure is also somewhat suggestive of conditions in a few of the tetrarhynchids (cf. Braun 1896:1293).

While the writer is not prepared to go further into this comparison he would like to emphasize the significance of the layers composing the walls of the bulbs in *H. globuliforme* in connection with the possible origin of these most aberrant structures. In discussing the homologies of the proboscides of the Trypanorhyncha Benham (1901) said: "It appears more probable (Pintner) that each proboscis has been developed by the deepening and modification of an 'accessory sucker' of some Tetraphyllidean as its relation to the bothridia and its mode of development closely agrees with these structures. Functionally too it is a perfection of the armature plus the accessory sucker of three forms [Acanthocephala, Nemertini, and Taenioidea]; whilst there is no doubt that the 'phyllidea' of the orders are identical." The fact that here the walls of the bulb, since they are composed of an outer layer of longitudinal muscles, a middle layer of circular fibres and an inner cuticular layer are not only comparable but directly continuous with the cuticula and cuticular muscles of the body wall and in the reverse order would seem to lend support to

Pintner's view. Simple invagination of the external layers of the body wall in development would account for these structures, while the proboscis with its retractor muscles might well be formed by the modification of the external layers of an "accessory sucker."

CYATHOCEPHALINAE Lühe 1899, e.p.

Scolex unarmed, not longer than broad, with two surficial sucking grooves, more or less fused with one another, or a single terminal one having a sucker-like structure. External segmentation little expressed or absent. Genital organs in each segment simple. Genital openings surficial, median. Vagina and uterus open into a common vestibule—in young proglottides near one another—lying behind the male opening and similar to the genital atrium of other cestodes, which may be surrounded by a sphincter-like musculature. The genital openings of the different segments do not open on the same surface, but alternate irregularly from one surface to the other. Uterus a coiled canal without uterus-sac. Sexually mature in the intestines of fishes.

Type genus: Cyathocephalus Kessler.

The above is Lühe's (1910:22) diagnosis modified to read "may be surrounded, etc." instead of "is surrounded, etc." in connection with the genital sphincter, since there is no such structure in the species described below.

CYATHOCEPHALUS Kessler 1868

Taenia (part.)	Pallas	1781
Taenia (part.)	Batsch	1786
Echinorhynchus (part.)	Zeder	1803
Cephalocotyleum	Diesing	1850
Cyathocephalus	Kessler	1868
Cyathocephalus	Grimm	1871
Monobothrium	Grimm	1871
Acrobothrium	Olsson	1872
Cyathocephalus	Zschokke	1884
Cyathocephalus	Loennberg	1889
Cyathocephalus	Kraemer	1892
Cyathocephalus	Olsson	1893
Cyathocephalus	Lühe	1889
Cyathocephalus	Braun	1900
Cyathocephalus	Lühe	1900
Cyathocephalus	Lühe	1910

Scolex a single, undivided, terminal, sucking organ, which in its form and structure no longer shows an origin from two fused surficial bothria. External segmentation only slightly indicated. Sphincter surrounding the female genital cloaca apparently little developed. Occurrence: In Teleosts.

Type Species: *C. truncatus* (Pallas, 1781).

CYATHOCEPHALUS AMERICANUS Cooper 1917

[Figs. 11, 82, 93, 99, 104]

? 1898	*Cyathocephalus truncatus*	Linton	1898:428
1917	*Cyathocephalus americanus*	Cooper	1917 : 35

Specific diagnosis: With the characters of the genus. Small cestodes, up to a length of at least 11mm. with a maximum breadth of 1.2mm. Scolex

funnel-shaped, 0.3 to 0.6mm. long and 0.5 to 0.9 broad, with revolute edges. Neck 1.0 to 1.8mm. in length. Segments twice as broad as long, terminal one rounded.

Cuticula 5 to 6μ in thickness, with neither hooks nor spines; subcuticula 25 to 50μ.

Ten to twenty sets of genitalia, beginning 1.5 to 2.0mm. from the anterior end. Strong tendency for the reproductive apertures to lie all on one surface of the strobila. Vagina opens behind the uterus. Neither papillae nor sphincters around the genital openings.

Testes in two lateral fields in the medulla of the anterior portion of the proglottis, 60 to 70μ in diameter. Coiled vas deferens anterodorsal to cirrus-sac; no seminal vesicle before entering cirrus-sac nor connective tissue sack surrounding the whole duct. Protruded cirrus 0.2mm. in length by 0.12 in diameter at base. Cirrus-sac ovoid in shape 0.20 to 0.23mm. in length by 0.17 in diameter; no retractors connecting it with the dorsal body-wall; large mass of glandular pigmented cells surrounding it dorsally and laterally.

Vagina 12 to 15μ in diameter; no sheath near its opening; receptaculum seminis 50 to 75μ. Spermiduct very short and narrow, 25 and 8μ respectively. Ovary tubulolobular, fan-shaped; wings extending dorsally and laterally around the ventral genital ducts; isthmus prominent, 0.18 by 0.10mm.; ova in same 13 to 15μ in diameter. Oocapt 25μ in diameter. Vitelline follicles continuous from proglottis to proglottis, forming a layer 90μ thick in the cortical parenchyma, 20 to 35 in transections. Shell-gland dorsal. Uterine rosette not surrounded by a muscular sac, but the organ is enveloped proximally by numerous glandular cells.

Eggs, 40 by 30μ.

Habitat: In stomach, pyloric ceca and intestine of the host.

HOST	LOCALITY	COLLECTOR	AUTHORITY
(?)*Coregonus clupeiformis*	Outer Id., L. Superior	J. W. Milner	Linton 1898 : 429
" "	Off Giant's Tomb Id., Georgian Bay, L. Huron	Cooper	Cooper (the present paper)
" "	Charlevoix, Mich.	"	"

Type specimen: No. 165A, in the writer's collection.
Co-type: No. 165B, in the collection of the University of Illinois.
Type locality: Georgian Bay, Lake Huron, off Giant's Tomb Island.

Altho the species described here is closely related to *C. truncatus* of Europe, it presents so many differences from that species, even barring some probable errors by Kraemer (1892), that it is considered to be new. Probably the same form was reported by Linton (1898:428).

As shown in the appended table where the largest specimens at hand are dealt with, this species is considerably smaller than the European species which ranges from 6 to 40mm. in length by 1.5 to 4 in width. Linton gave these measurements as 7 and 1.2mm.

The general shape of the body, however, is the same, as are the proportions of the scolex and proglottides. The border of the infundibuliform scolex (Fig. 11) is thickened and almost constantly rolled backward slightly as in the figures given by Zschokke (1884a, Fig. 9) and Kraemer (1892, Fig. 5). The funnel is about 0.22mm. in depth, and is usually filled with a plug of mucous membrane from the host's alimentary tract. The posterior limits of the scolex are difficult to define since the organ gradually narrows down and then as gradually enlarges again to form the neck. The latter is considered to include that portion of the anterior end of the worm between the narrowest region behind the scolex and the first vitelline follicles which are situated some distance ahead of the first cirrus-sac. The maximum breadth of the strobila is at the posterior end of either the first third or one-half. The segments are as described by various writers for *C. truncatus* about twice as broad as long, the last one, however, being rounded posteriorly and provided with a notch in the middle which accommodates the exit of the excretory vesicle. They are, furthermore, closely united, as pointed out by Linton (1898:429) when he said "The bodies of these specimens appear to be unsegmented, or, at least, with only very faint indication of division into segments." As a matter of fact numerous transverse wrinkles present in most specimens make it almost impossible without the external evidences of the inner genitalia to distinguish the limits of the proglottides. And in this respect they agree with *C. truncatus*, since Zschokke (1884:38) said concerning the segments: "Ils sont solidement fixés les uns aux autres, leurs limites sont difficilement visibles." The following table gives the measurements of four of the largest specimens studied:

Length	10mm.	9mm.	11mm.	7.5mm.
Maximum breadth	1.01	0.92	1.11	1.05
Length of neck	1.48	1.00	1.48	1.8
Breadth scolex, tip	0.55	0.53	0.74	0.64
" " , base	0.37	0.42	0.55	0 30
Length of scolex	0.42	0.33	0.61	0.50
Number of sets of genitalia	13	12	13	10
First cirrus from ant. end	1.85	1.66	2.25	2.01
Remarks	Toto	Toto	Toto	Sectioned

The cuticula is 5μ in thickness over the scolex as well as on the segments, and is divided into two layers, the outer of which is about one-half as thick as the inner and more or less irregular in structure. However, no such chitinous hooks as described by Kraemer (1892:10) for the cuticula of the lateral borders were seen, but the whole tissue is freely pierced with numerous foramina secundaria of the excretory system, which in *C. truncatus* Kraemer considered

to be the points of entrance of nutriment. The thickness of the cuticula, according to the same author, is 19μ, an outer irregular layer being 5μ and showing a sort of ecdysis ("Hautungsprocess"). This, however, may be simply the separation of the outer layer of the cuticula from the inner which often appears in sections, since he said, "Diese Auffassung wird dadurch erhärtet, dass sich an einigen Stellen dieser Belag nicht findet, dafür eine junge homogene Cuticula,"—the latter being then the inner homogeneous layer. At any rate, it is quite evident that the cuticula of *C. truncatus* is a much thicker tissue than that of the form described here—and no one else than Kraemer seems to have described it.

The subcuticula is comparable to that of *C. truncatus* in that it varies in thickness from 25 to 40μ. It is composed of considerably elongated columnar cells whose nuclei, 5μ in diameter, are as thick as the cells themselves. Scattered spaces in the loose parenchyma, which evidently accommodated calcareous bodies before they were dissolved in the fixing fluid, were found to be ellipsoidal to almost spherical in shape and to vary from 13 to 25μ in length by 7 to 18 in width. Linton stated that the calcareous bodies of *C. truncatus* are 10 to 20μ long, Zschokke that they are 8 to 10μ and Kraemer that their size is 30 by 18μ.

In general the musculature is as described by Kraemer, but all the groups are comparatively weakly developed (Fig. 82). The longitudinal layer, for instance, is only 20μ in thickness in the median line posteriorly and about 60μ in the neck region (76μ in *C. truncatus*) where the dorsoventral and transverse fibres are also much stronger than elsewhere. In the anterior part of the neck, particularly immediately behind the scolex, the fibres of the two latter series are much stronger, altho less numerous than farther back. Just ahead of the posterior end of the funnel they become arranged in an arcuate manner longitudinally as well as transversely. Then from there on to the tip of the scolex they gradually become more numerous as they concentrate around the funnel of the organ, of which they obviously act as constrictors. Antagonizing these are numerous weaker radial fibres, arranged as in *C. catenatus* Riggenbach (=*Diplocotyle rudolphii* Mont.) where they were considered by Riggenbach (1898:639) to be derived from the longitudinal muscles with which they are continuous at the base of the scolex. Altho they mingle freely among the latter, they are still quite separate from them. Thus the writer is inclined to the same view regarding their homologies in *C. americanus*, since it seems clear that the dorsoventral and transverse fibres, which might otherwise be considered to give rise to them, become modified to form the circular muscles of the scolex. As a matter of fact only a very few of the longitudinal muscles of the neck pass for a short distance beyond the bottom of the funnel; most of them are inserted in the latter, thus functioning with the radial fibres in enlarging the organ of adhesion. According to Riggenbach these radial muscles are apparently absent from *C. truncatus*. They were not described by Kraemer; but the enlargement of the funnel was considered to be accomplished by the contraction of the dorsoventral fibres (cf. his Fig. 1). The outermost layer of

circular and longitudinal muscles in the scolex, which are merely extensions of the cuticular muscles of the neck region, are not nearly so strongly developed as in *C. truncatus*. There is, however, in the neck region, particularly in its anterior portion, a series of outer longitudinal muscles which, altho situated in transections among the outer clear ends of the subcuticular cells and very close to the longitudinal cuticular fibres, are nevertheless quite distinct from the latter. At the base of the scolex they pass inwardly between the cells of the subcuticula and continue farther towards the anterior border of the funnel than do the inner or main longitudinal fibres. Posteriorly they diminish considerably in number but may readily be seen in the mature proglottides.

The nervous system is arranged in general as in *C. truncatus*; but the longitudinal trunks are only 26μ thick by 13 wide (0.345mm. according to Kraemer). In the neck they are scarcely enlarged to form ganglia, such as shown in Kraemer's Fig. 5, but each is divided into two distinct dorsoventral halves which gradually diverge as they pass on into the scolex to form four large nerves. There is no single transverse commissure connecting the main trunks behind the funnel of the scolex but instead a number of fine cross-connections which are often difficult to make out satisfactorily.

As regards the excretory system there is an inconstant number of longitudinal vessels in transection, evidently more than the six of *C. truncatus*, which do not occupy definite positions but anastomose freely with each other especially in the lateral portions of the medulla. In the scolex these vessels are smaller and the anastomoses are much more numerous, while posteriorly at least two pass into a quite irregularly shaped terminal vesicle, which, however, in the light of Wolf's (1906) findings cannot be considered to be a true terminal excretory vesicle. As above stated, foramina secundaria are quite numerous in the cuticula.

The reproductive organs appear quite close behind the neck, the vitelline follicles being situated from 1.3 to 2.3mm. from the anterior border of the scolex, and the first cirrus-sacs from 1.6 to 2.2mm. From 10 to 20 sets of genitalia were observed for this species. These follow each other closely and are not separated by any septa or other boundaries, the vitelline follicles being, in fact, strictly continuous from proglottis to proglottis. The openings of the cirrus-sacs vary from 0.45 to 0.75mm. apart, but as pointed out by Kraemer, these measurements are of little diagnostic value on account of the different states of contraction. As in *C. truncatus* the reproductive openings are all on one surface of the proglottis but alternate as a unit irregularly from one surface to the other. There is, however, a strong tendency for them to lie all on the one face of the strobila. This alternation also involves the ovary, the isthmus of which is arbitrarily considered in the cestode to be ventral. It usually lies on the same surface as the reproductive openings, so that when the latter passes to the opposite surface it moves accordingly. This alternation of the openings has, of course, been known ever since Pallas described *Taenia truncata* in 1781, but, so far as the writer is aware, no one has dealt with the relations between the openings and the ovary noted here. Concerning this matter Kraemer

said only: "Das Verhalten, dass die Geschlechtsorgane alternirend dorsal und ventral nach aussen münden, erinnert in gewisser Beziehung, an die alternierende marginalen Geschlechtsöffnungen verschiedener Fisch- und Vogeltaenien und wurde bereits von den ersten Beobachter, Pallas und Batsch erkannt, d.h., sie hatten auf beiden Flächen die fortlaufende Reihe der 'Punkte' wahrgenommen, ohne sie indessen als Ausmündungen der Sexualorgane zu deuten. Die neueren Beobachter haben sämmtlich dieses oben beschriebene Verhalten übersehen, und geben die Geschlechtsöffnungen als ventral gelegen an." But whatever is the stimulus which, during the very early stages of development of the sets of genitalia from their rudiments, causes the reversal of the whole proglottis, it would seem to be such at times as to fail to bring about the turning over of all parts of the rudiment. As shown in figure 104, which is a diagram of a sagittal series of seven proglottides including the terminal one, the cirrus and female genital cloaca of number three from the top have gone to the opposite surface while the ovarian isthmus, represented by the solid black disc in each segment, has remained on the same surface as those in segments 1, 2 and 4 in the immediate neighborhood. Here the stimulus which brought about the unisurficiality of the latter may have influenced the ovarian portion of the common rudiment of number three and caused it to lag behind, while the more peripheral rudiments of the cirrus, vagina and distal portions of the uterus were freer to move. This arrangement of the parts in the aberrant segment in question naturally causes considerable departures in the courses of the reproductive ducts from the normal.

The genital openings vary from 75 to 115μ apart, but again as pointed out by Kraemer these data are of very little specific value. The vagina and uterus open into a common genital sinus or cloaca, but unlike conditions in the European species the vagina opens constantly behind the uterus and slightly to one side and not ahead of it. Furthermore, neither papillae nor sphincter muscles are present around either or both genital openings in this species. The female genital cloaca, usually situated at the bottom of a depression and often on a low papilla, ranges from 30 to 60μ in depth. In frontal sections it is seen to be in the form of a transverse slit about 60μ in length, into the ends of which the vagina and uterus empty; that is, the vagina opens diagonally behind the uterus and usually to the right of it. It is lined by a direct continuation of the cuticula from the surface of the segment. The general habit of the reproductive organs is shown in figure 93, which is from a frontal section of a mature proglottis.

The majority of the testes are situated in the medullary parenchyma in two fields lateral to the cirrus-sac, or more strictly speaking, in the lateral portions of the region between the cirrus-sac and the ovary of the proglottis ahead, since they usually extend forward to the latter and backward to the anterior ends of the wings of the ovary of the segment to which they belong. While their shape is usaully spherical or somewhat flattened anteroposteriorly according to the condition of contraction of the segment, their maximum diameter is about 70μ. The coils of the vas deferens, altogether about 0.30mm. in dia-

meter, are accommodated in the somewhat confined space dorsal and anterior to the cirrus-sac, extending to the ovary ahead (Fig. 93). Whereas Kraemer gave the diameter of the duct as 0.133mm. or about eight times as large as just before it enters the cirrus-sac, it is only 45μ at the most in this species. Furthermore, it is not enlarged to form a seminal vesicle close to the cirrus-sac, as shown in Kraemer's figures 6 and 13, but gradually diminishes in size until as it pierces the wall of the latter its diameter is only 10μ. Nor is the whole vas deferens enclosed in a connective tissue sac, such as described by Kraemer. Within the pouch it enlarges considerably to form a thin-walled inner seminal vesicle, situated for the most part near the proximal end of the former but often lying alongside the cirrus proper. This portion of the duct may attain a diameter of 30μ even when empty. Then follows the cirrus proper which is sharply separated from the seminal vesicle; as a matter of fact it actually protrudes backward into the latter with a diameter of 10μ and for a distance of from 15 to 25μ. The extruded cirrus has a maximum length of 200μ, diameter at the base of 120μ, and at the tip of about 40μ. The thick cuticula covering the organ is decidedly roughened or irregularly "cleft," especially towards the tip, but not provided with spines of any kind. Incidentally, the protrusion of the cirrus on account of its size, results in the eversion of almost the whole of the contents of the sac. The length of the cirrus within the sac is at least 185μ, —it is usually bent once in its proximal portion—while its diameter varies considerably. The layer of parenchymatous and myoblastic nuclei surrounding the cirrus within the sac is about 10μ in thickness as compared with 5μ in *C. truncatus*. In sections of the extended cirrus most of these nuclei appear in the tip of the organ surrounding a good deal of the cuticula which still remains invaginated; but they are in all probability myoblastic as are others farther back along the course of the retractor fibres. In frontal sections the cirrus-sac is circular in outline (Fig. 93), its maximum diameter being 175μ, while in transverse and longitudinal sections it is oval in shape and the diameter (length of the organ) ranges from 200 to 230μ. The smaller end is directed ventrally. Its wall is comparatively thin, ill defined, and composed of a somewhat loose network of muscular fibres running irregularly obliquely in all directions, so that sections cut in any plane show them almost circularly arranged. Owing to this fact and to the further fact that its innermost fibres are not easily differentiated from the retractors of the cirrus proper which bulk largely in the contents of the sac, the wall is fairly difficult to locate with emission of the cirrus. The sac is furthermore not provided with any retractors connecting it with the dorsal body-wall as described by Kraemer for *C. truncatus*. Forming a sort of gland closely applied to that part of the cirrus-sac within the medulla there is to be seen, even in toto preparations, a comparatively large mass of large darkly pigmented polygonal cells (Fig. 93). In frontal sections they lie on each side of the sac but do not extend much beyond its anterior and posterior edges, the whole structure being thus shaped somewhat like a saddle. Each cell is elongate in shape provided with a well-defined wall, prominent tho not especially large nucleus, and very granular and highly pigmented cytoplasm,

the color of the pigment being dark brown. Altho they are very closely arranged around the wall of the cirrus-pouch and most of them are quite pointed towards the same, their function is pretty much a matter of conjecture; unless perhaps they are the much modified myoblasts of the muscles of the walls of the pouch. This is suggested by the intimate relations of the inner attenuated ends of some of them with the latter. No such cells have been described for the European species, so far as the writer is aware. It would seem, however, that certain "radiär gestellten, kolbenförmigen Drüsen," merely mentioned and figured by Linstow (1904:308, Fig. 26) as surrounding the cirrus-sac of *Bothrimonus pachycephalus* Linstow, are similar to these peculiar cells. But in the latter species they are evidently much less extensive than in *C. americanus*. Similar glandular cells were also described by Schneider (1902: 76) for *Bothrimonus nylandicus* Schneider.

From its opening which has been dealt with above the vagina proceeds dorsally almost at right angles to the surface of the proglottis, and then within the medulla turns backward with a few coils to expand into a comparatively enormous receptaculum seminis which, on account of its size, can scarcely be distinguished from one of the coils of the uterus. At the turn in its course the duct has a diameter of about 15μ and is lined with a continuation of the cuticula of the female genital cloaca, 5μ in thickness, and surrounded by a layer of circular muscles. As it passes above the ovarian isthmus its cuticular lining gradually diminishes in thickness, so that the seminal receptacle is provided with a very thin layer only. While the latter may have a diameter of 75μ slightly behind the isthmus of the ovary, it narrows down very abruptly before joining the oviduct to a very small spermiduct, 8μ in diameter and about 25μ in length. In distinct contrast with *C. truncatus* there is no "connective tissue and muscular sac" surrounding the beginning of the vagina, as described by Kraemer, but only the usual mass of nuclei, most of which are subcuticular in their nature. The ovary (Figs. 82, 93) is a tubulolobular organ, the limbs of which radiate from a ventral isthmus laterally as far as the nerve strands, anteriorly as far as the cirrus-sac, and dorsally thruout the whole of the medulla, thus surrounding the central connections of the genital ducts and the coils of the uterus (Fig. 93). The wings, in whose irregularly shaped tubules young ova in various stages of development are to be seen, connect with the rounded isthmus by narrow portions quite as described and figured by Kraemer, altho he evidently erroneously called the isthmus the "ootyp." The latter in this species has a width of 0.18mm. by a length of 0.10 as compared with the similar measurements of 0.19 and 0.07mm. in the case of *C. truncatus*. Ova from the isthmus measured from 13 to 15μ in diameter, their nuclei 7 to 8μ and their nucleoli 4μ, those of the latter species being 9 to 12μ according to Grimm (1871) and 15μ according to Kraemer who gave the diameter of their nuclei as 9μ. The oviduct begins with a rather short oocapt (Fig. 99), 25μ in diameter, and proceeds for only a comparatively short distance, with a diameter of from 15 to 20μ, before being joined by the spermiduct. A little farther dorsally it is met by the vitelline duct which comes from the ventral portion of

the medulla just ahead of the isthmus where it is formed by the union of a right and left duct as in *C. truncatus*. Thruout its dorsoventral course the vitelline duct is expanded to form a vitelline reservoir which may reach a diameter of 40μ. Immediately outside of the longitudinal muscles the vitelline follicles form a compact layer from 70 to 90μ in thickness (152μ in *C. truncatus*), continuous from proglottis to proglottis and broken only immediately around the reproductive openings. They range in diameter from 30 to 85μ, while their number in transverse sections varies from 20 to 35, 45 being given by Kraemer. From its point of origin to a short distance beyond the entrance of the vitelline duct, the oviduct is lined with epithelial cells showing prominent nuclei but indistinct boundaries, the whole being thus of the nature of a syncitium. But soon this epithelium becomes modified in that, as the duct continues with a few coils to the opposite side of the proglottis, its cytoplasmic portion gets quite thin, while the nuclei remain more nearly the same size relatively speaking. Then as it further enlarges dorsally the oviduct is surrounded by an inconspicuous shell-gland. However, no shell-gland such as described by Kraemer was found in this species. Beyond the ootype the duct, in reality the beginning of the uterus, is enveloped for a considerable distance by numerous unicellular glands which at first sight appear to constitute a second and voluminous shell-gland. This mass of glandular tissue is so extensive in fact, that it occupies in frontal sections about one-half of the posterior half of the uterine rosette (Fig. 93). The individual cells, of which it is composed, are comparatively short, stout and well defined, their nuclei being large and the nucleoplasm clear like the cytoplasm. Most of the coils of this tubular uterus, which may attain a diameter of 0.10mm. or more when filled with eggs (0.038mm. in *C. truncatus*), are situated just behind the cirrus-sac. Before reaching the opening, the position of which has been stated above, the tube narrows down quickly. Thruout its course it is lined with a much attenuated epithelium, the nuclei of which, however, stand out prominently towards the lumen. In this species there is no muscular sac surrounding the uterus, as described and figured by Kraemer.

The largest eggs in the uterus not in a collapsed state were found to be ellipsoidal in shape and 40 by 30μ in size. Linton gave their size when preserved in acetic acid as 50 by 32μ; while the measurements for *C. truncatus* have been given as 95 by 76μ (Kraemer) and 44 to 51 by 33 to 36μ (Lühe, 1910). Since most of the eggs seen in the uteri of the sections made were quite young, many of them not having gone thru the first cleavage as yet, the writer is of the opinion that the size of the egg of this species is probably about the same as that given by Lühe for *C. truncatus* in Europe.

Altho evidently no one has as yet studied the early stages in the development of *C. truncatus*, Wolf (1906) discovered that the intermediate host is *Gammarus pulex* and that the transfer to the final hosts is a direct one. As regards the life history of *C. americanus* the writer can only say that he is of the opinion that *Pontoporeia hoyi* (Stimpson Mss.) may later be found to be the intermediate host at least in Georgian Bay, Lake Huron, where it constitutes practically the only food of *Coregonus clupeiformis*.

In the above description it has been shown that this species differs from the well-known *C. truncatus* of Europe in a great many points, but in none so radically as the following: The absence of chitinous hooks on the cuticula of the lateral borders; the presence of radial muscles in the walls of the scolex, and of a number of fine nerve commissures connecting the chief nerve strands anteriorly instead of a single one; the vagina opening behind the uterus opening; the absence of papillae and sphincter muscles surrounding the genital openings; no enlargement of the vas deferens to form a seminal vesicle just before entering the cirrus-pouch; no connective tissue sac surrounding the whole of the coiled vas deferens; the absence of dorsal retractor muscles of the cirrus-sac, and the presence of the peculiar glands closely surrounding the pouch; no "connective tissue and muscular sac" surrounding the beginning of the vagina; the very different central connections of the genital ducts as regards the ovarian isthmus ("ootyp" of Kraemer); and lastly, the absence of any such "shell-gland" as described by the same author. Consequently it has been considered to be specifically different from the European form and given a new name.

The material studied consisted of three lots, Nos. 43, 165 and 382A of the writer's colllection from the stomachs and intestines of several specimens of *Coregonus clupeiformis* (Mitchell) from Lakes Huron and Michigan as listed above.

BOTHRIMONUS Duvernoy 1842, char. emend.

Bothrimonus	Duvernoy	1842
Bothrimonus	Dujardin	1845
Bothrimonus	Diesing	1850
Cephalocotylea	Diesing	1850
Disymphytobothrium	Diesing	1854
Diplocotyle	Krabbe	1874
Diplocotyle	Monticelli	1890
Bothrimonus	Monticelli	1892
Diplocotyle	Braun	1900
Bothrimonus	Braun	1900
Diplocotyle	Lühe	1900
Bothrimonus	Lühe	1900
Bothrimonus	Schneider	1902
Diplocotyle	Linstow	1903
Bothrimonus	Linstow	1904

Scolex with two surficial and almost spherical bothria whose forwardly directed apertures may be separate or more or less completely fused to form a single terminal opening, according to the degree of contraction of the ridge separating the two internally, the latter representing the tip of the scolex in other bothriocephalids. External segmentation completely absent. Female genital cloaca with more or less well developed sphincter. Vitelline follicles in the cortical parenchyma in two lateral fields.

Occurence: In species of Acipenser and in teleosts.

Type species: *Bothrimonus sturionis* Duvernoy.

As pointed out by Schneider (1902a:72) the two genera Bothrimonus and Diplocotyle were separated by Lühe (1900:10) only on the basis of the differences in degree of fusion of the apertures of the bothria at the tip of the scolex. As a matter of fact the remainders of the generic diagnoses are identical. Schneider stated that the material of his *B. nylandicus* showed that these differences were simply due to differences in degree of contraction and relaxation of the scolex and in particular of its termination which is the ridge separating the two openings of the bothria either externally or internally. With considerable retraction of this ridge or septum the two openings fuse to form one, while with relaxation of the same and contraction of the bothrial walls the apertures are more or less separate, according to the species present. While in none of the few specimens of the species described below were the openings fused, various stages in the formation of a single terminal and almost circular opening from the two otherwise separate openings were observed in some material from *Microgadus tomcod* which was, however, too young to be determined with certainty specifically. Consequently, it seems just with the present state of our knowledge of these forms to unite the two genera, Bothrimonus and Diplocotyle, and to retain the older name of Duvernoy, as done by Schneider but not recognized by Linstow (1903; 1904:308).

BOTHRIMONUS INTERMEDIUS Cooper 1917

[Figs. 6-8, 45, 81, 94]

1917 *Bothrimonus intermedius* Cooper 1917 : 35

Specific diagnosis: With the characters of the genus. Small cestodes up to 45mm. in length and 1.6 in breadth. Scolex almost spherical, 0.60mm. long, 0.75 wide and 1.0 thick. Bothria hemispherical, their apertures ordinarily not fused to form a single terminal opening. Strobila uniform in width from a short distance behind the scolex to the posterior end; 0.6mm. in thickness; more convex ventrally than dorsally.

Cuticula 5μ in thickness. Nerve strands 15 to 20μ in diameter; each divides into two branches sagittally before entering the scolex; transverse commissure diffuse. Four main excretory trunks in ripe proglottides, six farther forward passing into the scolex; all in the medullary parenchyma.

Reproductive organs 1.5mm. from scolex; up to 66 in number. Weak sphincter around the common female cloaca. Vagina opens close behind the uterine pore which is not quite in the median line.

Testes in two lateral fields and two layers between the excretory trunks, continuous from proglottis to proglottis; spherical in shape, 80 to 100μ in diameter. Coils of vas deferens anterodorsal to cirrus-sac, the duct 30μ in diameter. Cirrus-sac oval, 75 by 45μ; everted cirrus, 60 by 85μ.

Vagina 10μ in diameter; receptaculum seminis, 40 to 60μ; spermiduct, 10μ. Ovary crescentic in shape, wings tubulolobular; isthmus almost spherical, 0.1mm. in diameter. Oocapt 25μ in diameter, oviduct 15 to 20μ. Common vitelline duct 120 by 30μ. Vitelline follicles spherical, 60μ in diameter; in the lateral thirds of the strobila, continuous at the margins of the same and from

proglottis to proglottis. Shell-gland obscure. Uterus surrounded by glandular cells proximally; 0.25mm. in maximum diameter.

Eggs, 36 by 24μ in dimensions.

Habitat: In the intestine of *Pseudopleuronectes americanus* (Walbaum), the winter flounder, from Brandy Cove, St. Croix River, at St. Andrews, New Brunswick.

Type specimen: No. 206.1 in the writer's collection.

Co-type: No. 206.2 from the same, deposited in the collection of the University of Illinois.

Since 1842, when Duvernoy described *Bothrimonus sturionis*, the type species and the only one reported for America up to date from a specimen of *Acipenser oxyrhynchus* Mitchill (=*A. sturio* L.) collected by M. Lesueur in 1835, the following species have been found in Europe: *Diplocotyle olrikii* Krabbe (1874), *D. rudolphii* Monticelli (1890:205), *B. fallax* Lühe (1900b:257), *B. nylandicus* Schneider (1902a:72), *D. cohaerens* Linstow (1903:291) and *B. pachycephalus* Linstow (1904:307). As pointed out by Schneider (1902:77), *D. serrata* Linstow (1901:288) evidently does not belong to the genus at all. But with none of these could the material studied in connection with the present description be alligned. Altho it bears resemblances in individual points to *B. cohaerens* and to *B. pachycephalus*, doubtless owing to the fact that these have been better described than the others, including *B. fallax*, and closely approaches *B. nylandicus*, yet it is so different from the latter that it is considered to constitute a new species.

The scolex (Figs. 6-8,) is typical in that it is composed of two surficial and almost hemispherical bothria arranged in the usual manner. These are well separated not only posteriorly from the strobila but laterally from each other by distinct grooves as in *B. nylandicus*. In all of the specimens studied the apertures of the bothria, usually circular in shape and about 0.1mm. in diameter altho in a few cases somewhat elongated dorsoventrally, were distinctly separate. But since, as shown by Schneider, there is great variation in the extent of fusion of the two apertures owing to differences in degree of contraction even in individual species, this separation is not considered to be of specific, let alone generic, value. The compressed lumen of the bothrium has a transverse diameter of 0.3mm.; while the other measurements of the scolex are as given in the table below. The short unsegmented region between the scolex and the first set of genitalia, which has a length of about 1.5mm., may be considered to be a neck. Excepting for the openings of the reproductive organs and the protruded cirri, there are no external indications of segmentation. Internally this is also the case as regards the vitellaria and testes, which are both strictly continuous from proglottis (set of genital organs) to proglottis, as in the genus Bothriocephalus (*vide infra*). The strobila, which is quite uniform in diameter from the region close behind the scolex, is about one-half as thick as broad and slightly more convex ventrally than dorsally, as in *B. nylandicus*. None of the specimens at hand were complete posteriorly. The

following table gives measurements of the three largest specimens of the material studied:

Length	45mm.	38mm.	21mm.
Length of scolex	0.55	0.59	0.37
Length of bothria	0.64	0.72	0.66
Breadth of scolex	0.74	0.76	0.72
Depth of scolex	0.90	0.94	1.02
Width of strobila just behind scolex	0.87	0.87	0.74
Maximum breadth	1.34	1.34	1.60
Average breadth	1.16	1.16	1.2
Depth at middle	0.55	0.50	0.61

The cuticula is about 5μ in thickness not only over the general surface of the strobila but also in the interior of the bothria. In the latter situation it is divided into two layers comparable to those described by Schneider (1902a: 75) for *B. nylandicus*: an outer, occupying about three-fifths of the whole thickness and made up of comparatively long comidia or pseudocilia, and an inner, quite darkly staining stratum. Whereas Schneider stated that "Diese Härchen finden sich überall auf der ganzen Oberfläche des Cestoden mit alleiniger Ausnahme der beiden Hohlräume in den Saugnäpfen und der Rinne, welche den Scolex vom Rumpfe scheidet," the writer found that these were the very places the two chief layers were best seen.

The musculature is quite similar to that of *B. nylandicus* as described by Schneider. All of the series are about equally, but none strongly, developed and each consists of isolated fibres. The arrangement of the fibres in the scolex is quite like that of *Clestobothrium crassiceps*, there being, however, no sphincters controlling the openings of the bothria.

The main longitudinal nerves are situated in the median frontal plane and about two-ninths of the transverse diameter of the strobila from the margins, posteriorly as well as in the neck region. In transverse sections each strand varies considerably in size and shape, but it is constantly considerably compressed and has a transverse diameter of from 15 to 20μ. Anteriorly the system differs greatly from that of *B. nylandicus*. In the latter, according to Schneider, the chief strands bend outwardly at enlargements in the region between the scolex and body; and from each of these nerves are given off to the neighboring bothria and one main branch towards the tip of the region to unite with its fellow of the opposite side, thus forming a commissure which is bowed forward. In this species each main trunk divides from 0.25 to 0.40mm. behind the posterior borders of the bothria into two branches of equal size which continue forward in a strictly sagittal plane as they gradually enlarge. At about the middle of the bothria each of these four trunks gives off large branches to the lateral walls of the former, and then, while approaching the median line and partly fusing with its fellow of the opposite surface, sends off several small branches to those on the other side. The commissure is, therefore, not single but composed of a number of transverse connectives of varying size. The

transverse ridge between the bothria, which represents the tip of the scolex, is also supplied with a number of small nerves from this irregular commissure.

In ripe proglottides there are four main longitudinal excretory vessels situated roughly in the median frontal plane, two at the extreme margins of the medulla and two just within the nerve strands. Farther forward these divide into three on each side. The middle one of each lateral trio then divides dorsoventrally into two, while the innermost pair gradually diminishes in size and are soon lost. This leaves three on each side, arranged as a triangle with the base towards the median line and the apex outward. They pass into the scolex and anastomose to form an irregular plexus. But this arrangement of the main vessels is attended with a good deal of irregularity; nor is it the same on both sides of the median line. For *B. nylandicus* Schneider described only two main longitudinal trunks "which divide anteriorly into several canals and form numerous coils, especially in the suckers." The excretory system of *B. fallax* according to Lühe (1900b:257) is like that described here in that there is a triangle of vessels on each side anastomosing with each other and with the nearest ones of the opposite side; but in adition it shows two other vessels which " . . . verlaufen im Gegensatz zu den dünnwandigen Gefässen des Plexus im Inneren der Markschicht, in der frontalen Medianebene, und zwar der eine nach innen, der andere nach aussen vom Längsnervenstamm. Letzterer erinnert seiner Lage nach an die Verhältnisse bei den Dibothriocephalinen, insofern als die Mehrzahl der Hodenbläschen nach aussen von ihm liegt." It will also be seen that the arrangement of the excretory vessels in this species is quite different from that described by Linstow (1904:308) for *B. pachycephalus* Linstow, in which species there are fourteen main vessels situated in the cortical parenchyma among the longitudinal muscles. None of the specimens were complete posteriorly so that the disposition of the system in the true posterior end was not determined.

The reproductive organs appear about 1.5mm. behind the scolex almost completely developed. Their openings are in the median line and, unlike *B. sturionis* Duvernoy, all on the ventral surface, that is, on the same surface towards which the ovarian isthmus is situated (cf. *B. fallax* Lühe, 1900:10 and *Cyathocephalus americanus*, p. 57). Furthermore, while the male and female openings are from 0.09 to 0.22mm. apart, the sets of genitalia up to 66 in numbe, are 0.55 to 0.65mm. apart in the longitudinal direction, which distances are, however, of no great specific value owing to the different degrees of contraction and relaxation of the strobila. The female genital cloaca is an irregularly circular opening into which the vagina opens constantly close behind the uterus, as in *B. nylandicus*, but in the median line, the uterine orifice being in this case the one which is not exactly in line with that of the vagina and the cirrus but alternates irregularly from side to side. There is a weakly developed sphincter surrounding the common female cloaca. It seems, however, to be at least partly confined to the vaginal opening rather than to that of the uterus.

As in *B. nylandicus*, *B. pachycephalus* and *B. cohaerens* the testes are situated in the medullary region and in two narrow lateral fields continuous

from proglottis to proglottis. As a matter of fact, they are confined to the areas between the two pairs of the four main longitudinal excretory trunks mentioned above. They are usually almost spherical in shape with maximum diameters of 80 to 100μ. Transverse and sagittal sections show that, owing to the large size of the median reproductive organs, especially the large uterus, and their consequent inability to expand laterally, they are arranged in two pseudostrata which occupy the whole of the dorsoventral diameter of the medulla of the regions in question. These two tiers are, however, not nearly as extensive as in *B. pachycephalus* Linstow (1904:308, Fig. 26). The vas deferens is in the form of a narrow mass of coils, situated immediately anterodorsal to the cirrus-sac or slightly to one side, depending on the amount of distension and consequent approximation of the uterus of the same proglottis to that of the proglottis ahead. It also extends to the dorsal wall of the medulla; and its diameter is about 30μ. Just within the cirrus-sac the vas deferens is surrounded for a short distance by radiating gland-like cells, reminding one of those outside of the pouch in *C. americanus*. But there are no such cells outside of the cirrus-sac as described for *B. nylandicus* by Schneider. Then it gradually diminishes from a diameter of 35μ in the ejaculatory region, which immediately follows, or perhaps includes the glandular region, to about 20μ at the middle of the sac. From this point it enlarges quickly and takes on the cuticula and a series of circular muscular fibres to form the cirrus proper which in the distal portion of the pouch may attain a diameter of 50μ. The extended cirrus has a maximum length of about 60μ and diameter of 85μ. The cirrus-sac is oval in shape, the smaller end being outward and the major axis at right angles to the surface. Its depth is 0.25mm. while its diameter is 0.17mm. As in *C. americanus* its muscular walls are only weakly developed and hence not very distinctly separated from the parenchymatous tissue within and without. Apart from the duct the contents of the pouch consists of numerous parenchymatous cells and retractor muscles, the whole forming a quite compact structure.

Just within the medulla the vagina turns backward and continues ventrally and posteriorly with a few coils toward the ovarian isthmus. Whereas its diameter is 30μ near its opening, half way along its course this is reduced to 10μ and enlarged again to 40 to 60μ to form the seminal receptacle. Close behind and somewhat dorsal to the isthmus it again becomes sharply restricted to 10μ to form the spermiduct. Its whole course is quite as described for *B. nylandicus*; but in the latter there is evidently no enlargement to form a seminal receptacle or it was overlooked by Schneider, as indicated in his statement: "Sie passiert gleichfalls auf dem kürzesten Wege die Subcuticularschicht und die Muskelschichten, biegt dann in stumpfem Winkel nach hinten um und zieht, immer enger werdend, gegen den Ovidukt hin. In der Nähe des Eileiters wird sie so eng und dünnwandig, dass die Einmündungsstelle nicht genau festgestellt werden konnte." The ovary is like that of *B. nylandicus* in that it is crescentic in shape, the tubulolobular wings extending to the dorsal musculature and surrounding the uterine coils. It is, furthermore, comparable

to *C. americanus* in that these wings also pass forward from the isthmus—but only halfway along the sides of the uterus—and that the median region of the latter is spherical and somewhat larger than the lateral portions. From the anterodorsal aspect of this enlargement, which has a diameter of about 0.1mm., the oviduct arises as described and figured for *B. nylandicus*. The diameter of the oocapt is about 25μ, while that of the oviduct beyond its point of union with the spermiduct is from 15 to 20μ. The common vitelline duct, formed by the union close within the ventral musculature of a right and left duct, has a diameter of 30μ when filled with the yolk cells. The whole of the common duct, 0.12mm. in length, acts as a vitelline reservoir, while the right and left ducts usually contain a good deal of yolk close to their junction. As in *B. nylandicus* the vitelline follicles are arranged in two lateral fields in the cortical parenchyma, which are not only so restricted as to leave wide median areas free of them dorsally and ventrally but are continuous at the margins of the strobila as well as from proglottis to proglottis. Like the testes they are spherical in shape, closely arranged, and have maximum diameters of 60μ. The shell-gland, located just beyond the point of union of the common vitelline duct with the oviduct, is so weakly developed that it is all but absent. The opening of the common vitelline duct into the oviduct was not found to be "from the right side" as in *B. nylandicus* but irregularly from either side. Nor was there seen any distinct enlargement of the oviduct in the region of the ootype.

The first portion of the uterus is very thin-walled, and, especially when free of eggs, quite distinct from the distal portion which attains a diameter of 0.25 mm. The whole duct is so voluminous when filled with eggs that it occupies almost the whole of the medullary region of the proglottis and hence more than one-third of the transverse diameter and closely approximates that of the proglottides ahead and behind, thus crowding the other organs almost to the point of obliteration—and this in spite of the fact that its coils, mostly arranged in the sagittal direction, are very close together. The distal end of the duct gradually narrows down in passing ventrally to a diameter of from 35 to 45μ as it pierces the ventral musculature to open ahead of the vagina as above mentioned. No special enlargement of the tube just before its opening, such as was described for *B. nylandicus* is present in this form; but a considerable length of the proximal portion of the duct is surrounded by glandular cells quite similar to those of *C. americanus* (cf. p. 61).

The maximum dimensions of the eggs are 36 by 24μ as compared to 40 by 25μ in *B. nylandicus*.

As the above description indicates, this form comes closest to *B. nylandicus* Schneider, but it differs from that species in the following important points: It is considerably larger; the cuticula lining the bothria is the same as that covering the general surface of the strobila; the number and arrangement of the excretory vessels are quite different; the structure of the nervous system especially anteriorly is radically different; there are more than twice as many sets of genitalia; there are no gland-like cells just outside of the cirrus-sac; the vagina is expanded proximally into an elongated seminal vesicle; the open-

ing of the common vitelline duct into the oviduct is not from the right side only but from either side; the opening of the uterus, and not that of the vagina, is not strictly median but alternating irregularly from side to side, while there is no enlargement of the uterus just before its opening; and finally, but of least importance, there is no fusion of the bothrial apertures. Consequently it seems fitting to consider this form a new species.

The material studied consisted of two somewhat fragmentary lots, Nos. 205 and 206 of the writer's collection, from *Pseudopleuronectes americanus* (Walbaum), the winter flounder.

MARSIPOMETRINAE Cooper 1917

Scolex with two typical and fairly deep bothria and a terminal disc. External segmentation very distinct and regular. Opening of cirrus and vagina marginal, irregularly alternating; uterus-opening surficial, ventral, at the same level with the genital cloaca or very slightly behind it. Only one set of genitalia in each proglottis. Testes in medulla between the nerve strands. Muscular vesicula seminalis outside of the cirrus-sac absent. Receptaculum seminis large, sharply separated from the spermiduct. Ovary not exactly in the median line but slightly approaching the margin bearing the genital cloaca, ventral, as is the shell-gland. Uterus in the form of a sac developed by the enlargement inwardly of that portion of the duct passing thru the cortical parenchyma. Eggs without opercula.

Type genus: Marsipometra Cooper.

As regards the general form of the scolex and the facts that the genital cloaca is marginal and that a vesicula seminalis is absent, Marsipometra comes closest to the Triaenophorinae; otherwise, however, it is related to other subfamilies. External segmentation is distinct and very regular, a neck being present as in Diphyllobothrium and Bothridium of the Diphyllobothriinae. The uterus-opening is at the same level with the genital cloaca, and not ahead of it as in the Triaenophorinae. Furthermore, as in most of the subfamilies there is only one set of genitalia in each proglottis. The testes are situated in the medulla between the nerve strands as in the Haplobothriinae. Unlike the structure in the Triaenophorinae, the receptaculum seminis is large and sharply separated from its continuation, the spermiduct, which also obtains for the Ligulinae, Haplobothriinae, Diphyllobothriinae and Cyathocephalus. The ovary is comparable to that of Triaenophorus, Anchistrocephalus and Anonchocephalus (cf. Lühe, 1902:325) in that it is not exactly in the median line but situated towards the margin bearing the genital cloaca. As in the Triaenophorinae, however, the uterus "nie die sogenannte Rosettenform bildend, vor seiner Mündung meist etwas erweitert, ohne dass indessen diese Erweiterung verhältnissmässig so beträchtlich ist, wie die sogenannte Uterushöhle der meisten Ptychobothriiden." This latter difference is further emphasized by the fact that at no stage in its development is the beginning of the uterus, which might be considered at first sight to be a true uterine duct, sharply separated from the enlarged portion as in the Ptychobothriidae. The outstanding feature that the eggs are nonoperculate has been noted under the remarks on the family.

MARSIPOMETRA Cooper 1917

Dibothrium	Linton	1897
Bothriotaenia	Ariola	1900

Scolex unarmed, sagittate. Neck present; strobila flat, ribbon-shaped: proglottides almost rectangular, posterior borders only slightly projecting.

Nerve strands far towards the margins, dorsal to the cirrus-sac and vagina. Testes in two lateral fields united ahead of and behind the uterus-sac and central genital ducts. Vas deferens much coiled proximally, only weakly so close to the cirrus-sac. Receptaculum seminis very long. Ovary reniform, wings tubulolobular, isthmus thick. Shell-gland not in the middle of the genital complex but towards the cloaca, ahead of the ovary. Vitelline follicles numerous, not in two lateral fields but continuous from side to side in the anterior and posterior regions of the proglottis, situated among the body muscles. Uterus-sac pouched, occupying the whole of the medulla dorsoventrally but not transversely. Uterus opening towards the margin bearing the genital cloaca.— *μαρσιπίον* a little pouch; *μήτρα* the uterus.

Type species: *M. hastata* Linton.

Attention is here called to the great similarity between Marsipometra and Haplobothrium in that each is found in an isolated genus of fishes, respectively Polyodon and Amia, which in turn are relegated to isolated families and orders. As suggested previously by the writer (1914) in dealing with Haplobothrium, the unique and generalized nature of these two genera is doubtless due to the great age of their respective hosts. On account of the fact that it has a typical bothriocephalid scolex, Marsipometra would seem to be the younger of the two, for evidently a longer period of time must have been required for the development of the peculiar trypanorhynchous scolex and method of segmentation of Haplobothrium, if indeed both are not due to extreme degeneration comparatively speaking.

MARSIPOMETRA HASTATA (Linton 1898)

[Figs. 4, 5, 46, 47, 68, 83, 100, 101]

1898	*Dibothrium hastatum*	Linton	1898:431
1900	*Bothriotaenia hastata*	Ariola	1900:440
1917	*Marsipometra hastata*	Cooper	1917:36

Specific diagnosis: With the characters of the genus. Medium sized cestodes up to a length of 110mm. with a maximum breadth of 3mm. at the middle. Scolex with deep bothria and prominent posterior borders, 1.5 to 2.8mm. in length, 0.5 to 1.8mm. in width anteriorly and 1.3 to 2.0 posteriorly. Subcylindrical neck, 0.8 to 1.5mm. wide. First segments very short and wide, middle much broader than long and rectangular in outline, posterior ones quadrate to slightly longer than broad. Whole strobila much depressed.

Cuticula 5μ in thickness, subcuticula 40 to 50μ. Calcareous bodies 18 by 13μ. Longitudinal musculature weakly developed, that of scolex strong. Nerve strands 15 to 25μ in diameter. Four main excretory vessels in the strobila.

Genital cloaca 40 to 60μ in depth, at the middle of the margin of the proglottis, irregularly alternating; hermaphroditic duct present, also sphincter cloacae. Vagina opens immediately ahead of the cirrus.

Testes ellipsoidal, 60 to 90μ in diameter, 80 to 120 in number, arranged in a single layer in the medulla and interrupted only centrally. Vas deferens a circular mass of coils, 0.25 to 0.30mm. in diameter dorsal to the uterus-sac, or to one side of it. Seminal vesicle within the cirrus-sac, 50 to 60μ in diameter; cirrus proper slender, 0.20mm. in length, 8 to 15μ in diameter. Cirrus-sac elongate, flask-shaped, 0.35mm. in length, 110μ in maximum diameter.

Vagina 15 to 20μ in diameter; passes to median line ventrally, then dorsal to the uterus. Receptaculum seminis median, 90μ in diameter. Ovary reniform, tubulolobular, 0.45mm. wide and 0.18 long; isthmus thick, ventral. Oocapt 40μ long and 18 in diameter. Two ventral vitelline ducts; common vitelline duct 20μ in diameter. Vitelline follicles irregular in shape and size, forming a continuous layer around the proglottis excepting for median circular areas dorsally and ventrally. Shell-gland small, compact, 115 by 55μ. Uterine duct with only a few dorsoventral coils near the median line. Uterus-sac circular in outline, 1.0mm. in diameter, divided by deep incisions into 5 to 8 pouches; openings opposite the genital cloaca or slightly behind its level in gravid proglottides almost in the medial line.

Eggs, 45 by 36μ.

Habitat: Intestine of host.

HOST	LOCALITY	COLLECTOR	AUTHORITY
Polyodon spathula (type host)	Ohio R., Washington, Pa.	E. Linton	Linton 1898:431
" "	Ill. R., Beardstown, Ill.	H. J. Vancleave	Cooper (the present paper)
" "	L. des Allemands, Georgia	H. B. Ward	"
" "	Mississippi R., Keokuk, Iowa	H. B. Ward	"
" "	Mississippi R., Fairport, Iowa	H. B. Ward	"

Type specimen: No. 4724, Collection of the United States National Museum.
Type locality: Ohio River, Washington, Pennsylvania.

This species was originally described by Linton but with so little attention to the internal anatomy that up to the present it has remained pretty much a species inquirenda et incerta sedis, as pointed out by Lühe (1899c:40; 1900a: 106); altho Ariola (1900:440) placed it in the now obsolete genus Bothriotaenia Railliet.

Linton described the color of the living forms as " . . . at first lemon-yellow; after lying in water for a few minutes the bodies become colorless or faintly bluish translucent, while the heads remained yellowish." Regarding their method of attachment he said: "Two pits were found excavated in the mucous and submucous layers of the pylorus near the spiral valve, in which the heads of a number of *Dibothria* were inserted. The length of the worm was re-

corded by the same writer as from 25 to 78mm., while the maximum breadth was 2.7mm. As shown in the table below, the largest examined by the writer was one 110mm. in length with a maximum breadth of 3mm., which, however, showed the characteristic opaque white uterus-sac filled with eggs in only the last eight proglottides. The scolex (Figs. 4, 5) and strobila are, as described by Linton, ". . . sagittate (when at rest and contracted), terminated anteriorly with a button shaped tip [the terminal disc] which is bluntly rounded in front and marked off from the remainder of the head by a slight constriction, in life angled posteriorly; pits [bothria] variable in life but usually elliptical, often with anterior margin acuminate and sometimes with posterior margin indistinct. The head is angled posteriorly both laterally [surficially] and marginally, presenting a quite characteristic appearance in the living worm. Neck subcylindrical, narrower than the head. The segments begin some distance (6 or 8mm.) back of the head, as faint transverse lines. The first distinct segments are closely crowded much broader than long, median segments squarish [but still much broader than long], posterior segments usually a little longer than broad, rectangular, apparently separating rather easily. . . . Posterior angles of the segments slightly projecting. . . . Outline of most of the strobilas nearly linear and about the same breadth as the head. All the segments were remarkably regular in outline, no irregularities being observed." While this regularity in the form of the proglottides and in their gradual increase in size anteriorly and change of shape posteriorly is especially noteworthy in this species, the writer met with a few cases of intercalated triangular and aberrantly subdivided segments in the material studied. It should be emphasized, too, that the whole strobila including even the scolex is constantly much flattened dorsoventrally, which also assists in giving the worm the peculiar diagrammatic appearance which is mentioned below. The following table gives the measurements of four specimens, together with those by Linton in the first two colums for comparison:

Length	60mm.	45mm.	76mm.	39mm.	61mm.	110mm.
Length of scolex	2.75	1.85	1.48	1.75	2.34	2.01
Width term. disc	1.8	.....	0.60	0.55	0.73	0.80
Depth term. disc	.....	.....	0.43	0.31	0.60	0.42
Width at base	2.0	1.7	1.35	1.31	1.83	1.95
Depth at base	.....	1.3	1.16	0.96	0.98	1.10
Width of neck	1.1	.....	0.87	0.88	1.40	1.52
Depth of neck	.....	0.4	0.36	0.37	0.48	0.68
Length middle segs	.....	0.35	0.75	0.46	0.80	0.73
Width of same	.....	2.5	2.32	1.38	2.75	2.44
Length post. segs	1.13	0.55	1.5	0.85	0.90	1.52
Wikth of same	2.0	2.7	1.4	1.10	2.85	2.44
Maximum breadth	.....	.....	2.38	1.38	3.0	3.0
Measured in	water	alcohol	O.W.	O.W.	Alc.	Formol

The cuticula, 5μ in thickness, consists of two layers of equal thickness, an outer irregular and more darkly staining layer, which is sloughed off in many places, and an inner, more homogeneous and lighter stratum between which the outermost portion of the inner layer shows as a dark bounding membrane. Altho only about one-half as thick on the outside of the scolex and still thinner on the inside of the bothria, it is not modified to form minute spines on the edges of the terminal disc nor hinder end of the scolex where such might be expected to be located. Their absence also on the posterior borders of the proglottides (cf. *Haplobothrium globuliforme*) is not surprising since these protrude only very slightly. The subcuticula varies from 40 to 50μ in thickness and is made up of narrow elongated cylindrical cells with small nuclei, the outer ends of which are dendritic and quite separate from each other as are the bodies themselves. The meshes of the parenchyma are very loose and open, the spaces being large and the strands of the cytoplasmic framework considerably narrower than the small nuclei which are located as usual at the intersections but surrounded by only a limited amount of protoplasm. Linton stated that, "The segments contain numerous calcareous bodies, which exhibit a concentric structure." They are to be found fairly plentiful in all parts of the medulla and cortex and even among the subcuticular cells. They are elliptical or oval in outline, the largest having dimensions of 18 by 13μ.

The musculature of this species, excepting that of the scolex, is comparatively weak, no one series, not even the longitudinal, being especially strong. All groups are prominent, in that they consist of more or less isolated fibres quite diagrammatically arranged. Their conspicuousness is, indeed, amplified by the fine texture of the parenchyma. The frontal or transverse series do not form a compact layer closely applied to the inside of the longitudinal muscles but, as shown in figure 83, a stratum of varying thickness; owing to the degree of separation of the fibres, especially laterally. The myoblastic nuclei of many of them can be easily seen. The sagittal series are, however, quite prominent, and equally distributed from border to border of the strobila. They show their myoblastic nuclei and surrounding cytoplasm very clearly, reminding one of the dorsoventral muscles of *Abothrium rugosum*. While the fibres of both these series are only slightly more numerous opposite the posterior borders of the proglottides, where they form more or less distinct septa, they are very well developed in the neck and anterior segments. The longitudinal muscles form only a single layer of loosely arranged fascicles of irregular size in the middle and posterior segments, but in the neck they form a much thicker stratum, showing no distinct bundles and occupying the whole of the space between the transverse muscles and the subcuticular nuclei. Altho, as above mentioned, the posterior borders of the proglottides are not very prominent, there is a representative series of outer longitudinal muscles, best seen in the middle segments where they are situated close to the longitudinal cuticular fibres with which they are easily confused. Concerning the latter all that need be said is that they are well developed and consist of isolated fibres which render the two layers all the more visible.

The musculature of the scolex is, as might be judged from its size and its shape, very powerful. While the longitudinal muscles of the neck merely enter the base of the scolex, the transverse and sagittal fibres are directly continuous with the circular and radial fibres, respectively, of the latter. Here, however, the radial fibres are quite separate from the dorsoventral fibres with which they are considered to be homologous, especially laterally where they pass from the cuticula lining the bothria to the sides of the scolex as in other bothriocephalids with prominent bothrial walls. Farther forward the sagittal muscles proper passing between the bothria are scarce, their function being taken over by the very numerous and closely arranged radial fibres which are quite as plentiful in the median line as laterally. In the terminal disc both transverse and dorsoventral fibres are again prominent, while the radial ones are absent. Posteriorly the latter pass down along the sharp edges of the beginning of the neck. Frontal sections demonstrate the presence in the edge of the terminal disc as well as in the posterior borders of the scolex of two series of longitudinal arcuate fibres arranged for the control of these prominent ridges. These are perhaps modified portions of the outer longitudinal muscles which are very numerous in the scolex, and converge in the anterior portions of the edges of the walls of the bothria to become attached to the edge of the terminal disc at the four respective points.

The chief nerve strands, from 15 to 25μ in dorsoventral diameter and from 15 to 20μ in lateral diameter, are situated far towards the edges of the medulla and in the median frontal plane or somewhat dorsally (Fig. 83). They pass dorsal to the junction between the lateral and middle thirds of the cirrus-sac and consequently dorsal to the vagina. In the neck they are located in the very borders of the medullary parenchyma, but as they enter the base of the scolex they approach the median line somewhat. As they pass on with a varying diameter towards the tip of the scolex, they give off a number of branches to the walls of the bothria and finally enlarge in the terminal disc to form two ganglia, each with a diameter of about 50μ, which send off in turn numerous large branches to the immediate neighborhood. Each of these ganglia is divided into two large trunks which, however, continue only a very short distance farther forward before they are joined by two commissures to their fellows of the opposite side of the scolex in such a way that the two branches of the ganglia on each surface of the scolex are connected. In frontal sections each of these commissures is seen to be bowed slightly forward into the tip of the terminal disc and to give off further forward on each side a large branch which passes farther into the latter.

The excretory system consists of a varying number of vessels, of which four pursue a more or less constant course thruout the medulla of the strobila. These are found at all levels in transections and are separated from each other in the transverse direction by different distances. The outermost two, however, are slightly larger and have thinner walls than the innermost pair. They give off numerous large branches and are connected by various anastomoses with each other and the more peripheral vessels. In the neck they cannot be

followed as well, while close to the scolex they lose their identity and break up into a plexus of very small vessels which ramifies forward thruout the latter. In the posterior border of the scolex, however, a small branch on each side takes a straight course just within the nerve strand for a short distance. Flame-cells are quite numerous and readily discernible especially in the medullary parenchyma. In young strobilas where no segments have yet been lost, two comparatively large excretory vessels pass backward to the posterior end and empty into a small narrow terminal vesicle. This in a larva 12.4mm. in length was found to be 40μ long by 10μ wide, while the diameter of the excretory vessels was 15μ.

The earliest traces of the reproductive organs in the form of a transverse line in either half of the proglottis (the rudiments of the vagina, cirrus-sac and lateral portions of the vas deferens) appear from 4 to 10mm. from the tip of the scolex, while the first eggs are seen in the uterus-sacs from 25 to 35mm. from the same point. The development of all of the genitalia is very gradual and can be easily followed in good toto preparations, since the diagrammatic nature of the worm, above mentioned, extends to the reproductive system, making this species an ideal one for study. The cirrus and vagina open into a common genital cloaca, which is situated in the middle of the margin of the proglottis, while the uterus opens on the ventral surface, not in the median line but towards the side occupied by the atrium. The cloacae alternate irregularly from side to side, from one to ten having been found occupying the same margin in successive proglottides. The following figures represent the number of such segments before the genital aperture changes to the other side in the fifth specimen of the above table: 1, 2, 1, 8, 1, 1, 1, 2, 2, 3, 3, 1, 2, 2, 10, 1, 1, 1, 3, 3, 2, 2, 1, 4, 1, 1, 2, 2, 3, 2, 2, 3, 6, 6, 1, 1, 1, 1, 1, 3, 2, 1, 3, 3, 2—as far forward as the rudiments could be conveniently traced. The genital cloaca (Figs. 100, 101) is elliptical in outline when viewed from the side, its longer diameter being directed dorsoventrally, while in transverse sections it is squarish in outline. The dorsoventral diameter, longitudinal diameter and depth are, respectively, 70 to 85μ, 40 to 55μ and 40 to 60μ. Into the middle of the bottom of this depression opens the hermaphroditic duct which is about 60μ in length, into the bottom of which in turn opens the vagina immediately ahead of the cirrus. Since the cirrus proper is a long slender tube and since the external portion of the hermaphroditic duct is usually found quite tightly closed and the end of the cirrus turned around toward the opening of the vagina, self-impregnation would seem to be quite probable in this species. On the other hand, the fact that the genital cloaca is so well formed and further that it is surrounded by a well developed sphincter and a series of muscular fibres radiating out into the surrounding parenchyma, as shown in figures 100 and 101, argue in favor of its use in cross-fertilization. No protruded cirri were seen, however, in the material at hand. Perhaps both methods of fertilization occur.

The testes are spherical to ellipsoidal in shape, their longest diameters being dorsoventral, while their cross-sections are usually circular in outline. In segments where there are as yet only a few eggs in the uteri their dorsoven-

tral and transverse diameters are, respectively, 85 to 90μ and 60 to 80μ. In the anterior and posterior ends of the proglottis—they are not continuous from segment to segment but separated by the aggregations of sagittal and transverse muscles mentioned above as forming more or less complete septa—they form a single layer situated in the medulla in the median frontal plane, but are widely separated in the middle of the proglottis by the central genital organs and ducts, especially the uterus-sac. Their number ranges from 80 to 120 for each proglottis. While the wall of the testis consists of a very thin membrane from which nuclei protrude inwardly, the contents are such as to show the process of spermatogenesis quite clearly. The vas deferens forms a circular mass of coils, 0.25 to 0.30mm. in diameter, applied like a cap to the dorsal side of the developing uterus-sac and thus close to the inner end of the cirrus-sac. When the uterus becomes gorged with eggs it is pushed aside somewhat but still retains similar relations with one of the pouches of the former, located in the direction of the genital cloaca (Fig. 68). In the mass of coils the duct is usually distended with spermatozoa to a diameter of 40μ. It gradually narrows down to a diameter of 15μ before entering the cirrus-sac, before which there is, however, no seminal vesicle. But within the pouch the vas deferens enlarges to form a large seminal vesicle, which with a diameter of from 50 to 60μ takes only a few coils before passing on as the cirrus proper from which it is sharply separated (Fig. 101). The cirrus is a slender tube from 0.17 to 0.22mm. in length within the pouch and from 15μ in diameter nearest the seminal vesicle to 8μ at its opening. It is lined with a thin cuticula which is circularly cleft in its proximal one-third but almost smooth for the rest of its length, nowhere, however, showing anything in the nature of an armament. The cirrus-sac (Fig. 101) is an elongated flask-shaped structure with a maximum diameter proximally of 110μ and distally of 40μ, and a length of 0.35mm. The neck of the organ usually shows a couple of dorsoventral curves, while about 20μ of its distal end protrudes into the hermaphroditic duct. Its walls are comparatively thin and composed of an inner layer of circular muscles and an outer weaker and much less compact layer of longitudinal fibres. Apart from the seminal vesicle which occupies almost the whole of the proximal enlarged portion and the narrow cirrus, the contents consist of only a limited amount of parenchymatous tissue and a very few feeble retractor muscles. The whole structure of the cirrus-sac is in fact such as to suggest that the function is that of an organ for the explusion of spermatozoa rather than for the emission of a copulatory organ; altho a few muscles passing from the body wall around the cloaca to the anterior part of the neck of the sac (Figs. 100, 101) would seem to indicate that a small portion at least of the cirrus is protruded, perhaps during self-fertilization.

Altho the vagina opens into the hermaphroditic duct directly ahead of the cirrus, it almost immediately curves around the distal portion of the cirrus-sac to the anteroventral side of the latter which it follows closely towards the median line. Close to the wall of the inner end of the cirrus-sac, however, it crosses the distal coils of the vas deferens towards the dorsal sufrace and

skirts the uterus-sac. When it reaches the median line above the sack it turns sharply downward and backward. The vagina has a diameter of from 15 to 20μ opposite the middle of the cirrus-sac and is lined with only a comparatively thin layer of cuticula. It very gradually expands after crossing the inner end of the cirrus-sac to form a much elongated and very spacious receptaculum seminis, the diameter of which close to its inner end may be as much as 90μ. This is usually filled in sections with spermatozoa, a stream of which may often be seen passing on into the spermiduct. The beginning of the duct is surrounded by a poorly developed layer of circular muscles which are almost absent from the inner expanded portion. The receptaculum is sharply separated from the spermiduct which has a diameter of only 15 to 20μ and a length of 0.12mm. The latter is an almost straight tube passing in the median line from the more dorsally situated receptaculum to its point of union with the oviduct close to the ventral wall of the medulla (Fig. 83). It shows best in transections where its walls are seen to be composed of an epithelium of cubical cells lying on a distinct basement membrane, and to be surrounded with a thick layer of nuclei and extremely few, if any, muscle fibres. The ovary (Figs. 68, 83) is a somewhat kidney-shaped tubulolobular organ situated in the posterior half of the proglottis behind the developing uterus-sac with its concavity directed forward, and not exactly in the median line but slightly approaching the cloaca. It averages 0.45mm. in width by 0.18 in length. The isthmus, which is almost as long and about one-half as thick as the wings, is located only slightly below the median frontal plane of the medulla. Ova from the same have a diameter of from 20 to 25μ. In gravid proglottides where the uterus is filled with eggs only a small portion of the degenerating ovary remains, and this is accommodated between the two hindermost pouches of the uterus-sac. The oviduct commences in the median line anteroventral to the ovarian isthmus as a somewhat cylindrical oocapt, 40μ in length by 18 in diameter and not sharply separated from the rest of the duct (Fig. 83). It passes ventrally with a diameter of 20μ for about 50μ before being joined by the spermiduct, and then for only a short distance farther anterolaterally along the ventral transverse musculature before meeting the common vitelline duct. The latter is formed by the union in the usual manner of two vitelline ducts coming from the lateral regions of the proglottis along the ventral wall of the medulla. It is quite short, however, and usually contains only a limited amount of yolk, its diameter being at the most only 20μ. The vitelline follicles (Fig. 83) are irregularly ellipsoidal in shape, and situated either just within the transverse muscles, between them and the longitudinal muscles, among the latter or even slightly outside of the longitudinal muscles. While they vary considerably in size and, not being very numerous, are widely spaced, their average maximum diameter is about 50μ. They form a continuous band completely surrounding the medulla, excepting for irregularly circular areas above and below the ventral ducts and organs, in the median line, but are not continuous from joint to joint. On the whole they remind one of the vitellaria of *A. crassum*. The union of their different ductlets can be easily traced,

especially in frontal sections of younger proglottides, since they are comparatively large and hence quite distinct. The shell-gland is a small compact organ, about 115μ in width by 55μ in length, surrounding the oviduct just beyond the entrance of the vitelline duct, or to be more exact, just beyond the first turn taken by the latter in its return to the median line after passing laterally, as above stated. It is thus situated ventrally and a short distance from the median line. Beyond the shell-gland the oviduct continues as the uterine duct which takes only a few dorsoventral turns near the median line before emptying into the uterus-sac. The latter is formed in development by the gradual enlargement dorsally of that portion of the duct which traverses the cortical parenchyma on the ventral surface of the proglottis. Just before eggs appear in the sac this part of the tube can be seen in transections as a spindle-shaped dilatation, whose nucleated epithelial wall is surrounded by a thick layer of nuclei, the whole being, however, not distinctly separated from the proximal portion of the tube (the uterine duct of older stages) at a constriction just within the transverse musculature. In proglottides farther ahead this constriction is outside of the transverse muscles in the cortex; so that the uterus-sac must be looked upon, then, as being formed by a gradual enlargement of the distal end of the uterus as it becomes filled with eggs and not as a sac separated in the rudiments from the proximal uterine tract as in the Ptychobothriidae. In one case where only 5 or 6 eggs appeared in the lumen the uterus-sac had a diameter in frontal sections of 80μ; in the next segment following it was enlarged in all directions, somewhat elliptical in outline, with a diameter of 240μ; in the next still larger; and in the fourth somewhat pointed anteriorly. From this region on it quickly enlarges until finally it forms a capacious sac, as much as 1.0mm. in diameter, occupying in gravid proglottides the whole of the dorsoventral diameter of the medulla and almost all of the longitudinal and transverse diameters. In transverse sections it is almost entire in outline, while in frontal sections it is divided into from 5 to 8 large irregularly shaped lobes or diverticula, the hindermost two of which enclose the remainder of the ovary and the central connections of the reproductive ducts, as above mentioned. Ventrally, the sac is funnel-shaped towards the small opening which only appears when the proglottis becomes quite gravid. Since the uterus-sacs, even the most gravid ones, are not situated exactly in the median line but towards the margins bearing the genital cloacae, the openings form " . . . a zig-zag line of minute pores [which] traverses the median region of one of the broad faces of the strobila, each pore being near the middle of its segment." Linton correctly considered them to be for the escape of the eggs. Anteriorly, where the uterus-sacs do not yet contain eggs, these pores—in reality the ventral funnel-shaped portions of the sacs—are located about 0.18mm. on each side of the median line, but posteriorly they are relatively much closer together, in fact almost exactly in the median line. Furthermore, they are situated directly opposite or slightly behind the level of the genital cloaca. The opening is formed by the rupture of the body

wall in a very small and limited area, and not of a preformed membrane as in the Ptychobothriinae.

Concerning the eggs Linton (p. 433) said: "The ova are nearly spherical, with thin shells. They are about 0.04mm. in the greatest diameter." Those from material preserved in formalin were found by the writer to be sometimes spherical in shape but usually ovoid or ellipsoid, with maximum dimensions in the latter case of 45 by 36μ. Neither in sections nor in preparations of eggs from the uterus sacs of material in formol, alcohol or cleared in oil of wintergreen were opercula to be found, but at the one pole of the egg a small boss about 5μ in diameter which is often enlarged to form a distinct projection or appendage. Altho development had not progressed in any of the eggs studied so far that the six hooks of the oncosphere were visible, the writer is of the opinion that even in mature eggs no opercula would be found, since its almost spherical shape and the presence of the button-like thickening at one pole are quite like conditions in the nonoperculate egg of *Abothrium rugosum*, for instance, as described and figured by Schauinsland (1885:527) and further, since in the egg of the operculate type, as in that of *D. latum* or of *T. nodulosus*, described and figured by the same writer, the operculum is present long before the hexacanth embryo has developed.

As regards the life-history of this species nothing is as yet known. It is noteworthy, however, that very young larvae, such as shown in figures 46 and 47, can be easily recognized on account of the peculiar character of the scolex, so that it would not seem difficult to pick them out of the intermediate host whatever that may be. All sizes from the youngest (Fig. 46) to the largest were present in the material studied.

The material of this species consisted of Nos. 4724 and 4783 of the collection of the United States National Museum, Nos. 16.292, 16.421 and 17.11 of the collection of the University of Illinois and No. 154 of the writer's collection, all from the intestine of *Polyodon spathula*, the paddlefish.

TRIAENOPHORINAE Lühe 1899

Scolex armed or unarmed, always with two typical and not very deep bothria, ahead of which the flattened termination of the scolex projects more or less prominently in the form of a ring. External segmentation present or absent, in the former case an unjointed neck being absent. Opening of cirrus and vagina marginal, irregularly alternating; uterus opening surficial, ventral, ahead of the marginal genital aperture. Genital apparatus always single in each proglottis. No muscular bulb (Eschricht's body) on the inner end of the cirrus-sac. Receptaculum seminis comparatively small, not always sharply separated from the narrow inner end of the vagina. Uterus a much coiled canal, which while never forming a rosette is usually somewhat enlarged before its opening.

Sexually mature in the intestines of fishes and marine turtles; larval conditions mostly unknown.

Type genus: Triaenophorus Rudolphi.

TRIAENOPHORUS Rudolphi 1793

Vesicaria, Cysticercus et Taenia (omn. part.)	Auctorum	
Triaenophorus vel Tricuspidaria	Rudolphi	1793
Tricuspidaria	Rudolphi	1793
Triaenophorus	Rudolphi	1793
Rhytelminthus (part.)	Zeder	1800
Rhytis (part.)	Zeder	1803
Tricuspidaria	Rudolphi	1802
Tricuspidaria	Rudolphi	1809
Triaenophorus	Rudolphi	1809
Tricuspidaria	Rudolphi	1810
Tricuspidaria	Lamarck	1816
Triaenophorus	Rudolphi	1819
Triaenophorus	Creplin	1839
Triaenophorus	Dujardin	1845
Triaenophorus	Diesing	1850
Triaenophorus	Baird	1853
Triaenophorus	Molin	1858
Triaenophorus	Molin	1861
Triaenophorus	Diesing	1863
Triaenophorus	Olsson	1867
Triaenophorus	Lönnberg	1889
Triaenophorus	Olsson	1893
Triaenophorus	Lühe	1899
Triaenophorus	Lühe	1899
Triaenophorus	Braun	1900
Triaenophorus	Lühe	1900
Tricuspidaria	Stiles and Hassall	1902
Triaenophorus	Lühe	1910

Scolex armed with four three-pointed hooks, never replaced by a pseudoscolex. External segmentation completely absent. Longitudinal nerves dorsal to the cirrus-sac and vagina, close to the lateral borders. Testes between the nerve strands only, filling up the whole medullary parenchyma so far as this is not occupied by other organs; a testis-free middle field is quite as infrequently present as a pronounced dorsal layer of the testes. Coiling of the vas deferens in its proximal almost medially situated part, that portion passing distad to the cirrus-sac only very slightly coiled. Vitelline follicles form a continuous mantle between the subcuticula and the longitudinal musculature, which is broken only at the places where the genital ducts open. Ovary, approaching the lateral border bearing the genital openings, lies on the ventral transverse musculature, yet individual ovarian tubules extend partly thruout the whole medulla. Shell-gland just as infrequently median as the ovary lying behind it, also usually approaching the dorsal surface somewhat. First portion of the uterus only a weakly coiled canal (uterine duct) which passes thru the proglottis transversely and leads into a large single cavity (uterus-sac) which lies not exceptionally ahead of, but yet partly near the ovary, and usually not median but away from the margin bearing the genital openings. The latter also applies naturally to the uterus-openings which breaks thru later. Eggs thick-shelled, operculate.

Type species: *T. nodulosa* (Pallas 1781) Rudolphi 1793.

As indicated in the above synonymy the name Triaenophorus has absolute page priority altho Stiles and Hassall (1902:22) have contended that Rudolphi should not have changed the name of the genus in 1819 from Tricuspidaria to Triaenaphorus again, after having used it in connection with the specific description in 1810. The change has become so universally established in the literature that it does not seem justifiable to revert to the name Tricuspidaria which is known to only a comparatively small group of zoologists.

TRIAENOPHORUS sp. larv.

[Figs. 12-18]

Since all of the material at hand was larval, not even the earliest traces of the reproductive rudiments showing in toto preparations of the largest specimens, it was, of course, impossible to determine the species with certainty.

Two types of scolices are present, however, and these agree with the descriptions of the organ given by various authors for *T. nodulosus* (Pallas) and by Olsson (1893:20) and Fuhrmann (1910:88) in particular, for *T. robustus* Olsson. It will be seen also in the table below that these two forms are found respectively encysted in the liver, on the visceral organs, or in the wall of the stomach, and encysted in the muscles or free in the intestine of the hosts—in the latter case so firmly attached to the wall as to be deeply imbedded, the mucosa forming a protruding collar around the worm—the only exception being those from the intestines of *Esox masquinongy* and *Stizostedion vitreum* (*vide infra*). Olsson pointed out that these two species can be readily differentiated from each other on account of the situations in which they undergo their development. Whereas the larvae of *T. nodulosus* are found generally

within cysts in the liver of the intermediate hosts, as recorded by a number of writers, those of *T. robustus* are constantly encysted in large numbers in the flesh—Olsson having found them in *Coregonus albula* and *C. lavaretus*, Luther (1909:58) in *C. albula*, and Fuhrmann in the "brochet" (? *Esox lucius*).

The scolex of the *robustus* type (Figs. 12 and 13) is, as described by Olsson, in the form of a truncated rectangular pyramid, that part immediately behind the terminal disc being considerably constricted and more nearly elliptical in transverse section. As stated by Fuhrmann, "La limite posterieure du scolex de *T. robustus* est nettement marquée et les deux bothrias, l'un dorsal l'autre ventral, son très profonds. . . . " This delimitation of the scolex is emphasized by the fact that immediately behind the posterior border of the bothria the dorsal and ventral surfaces of the body of the larva are distinctly concave as are also the lateral surfaces, quite diagrammatically, in fact, as shown in the figures. These concavities extend farther back for a few millimeters and then gradually flatten out and pass insensibly into the convexities which together form the elliptical outline of the cross-section of the middle of the larva. And it should be emphasized that this was found to be a constant feature of all the material studied and not simply due to any possible local collapsing during dehydration. Altho, as shown in the table, the measurements of the whole scolex are much smaller than those given by Fuhrmann, as might be expected it is chiefly the structure and size of the trident of hooks that leads the writer to consider this type of larva to belong to *T. robustus*. Figure 14 of one of these compares very favorably with those shown in Olsson's figures 31 and 32 and Fuhrmann's figure 2, while the measurements (see table) quite agree with those given by the latter. The base of the trident is comparatively long or deep (in the sagittal direction), hence the specific name according to Olsson, while not only the full length of the larger hooks but also a good deal of the median ones project thru the cuticula as the functional tips. In figure 14, which is from an alcoholic specimen, these are seen to be darker than the basal piece. The following measurements are given for comparison with Fuhrmann's of adult specimens, which are placed alongside, the data in parentheses being of the opposite trident on the same surface of the scolex in question:

Host	*Esox lucius*		*Leucichthys artedi*		After Furmann
Length	147.5mm.	123.0m.	183.0mm.	47.0mm.	310-370mm.
Breadth (maximum)	1.07	1.16	0.98	1.10	4.00-4.50
Length of scolex	0.98	0.96	1.02	1.12	1.14-1.50
Breadth of term. disc.	0.77	0.83	0.84	0.84	0.95
Breadth of scolex posterly	1.05	1.07	1.30	1.08	1.40-1.50

Host	*Esolucius*		*Leucichthes artedi*		After Fuhrmann
Width of trident	0.31(0.30)	0.30(0.30)	0.32	0.28	0.29-0.32
Length, mediad	0.25(0.24)	0.23(0.23)	0.27	0.22	0.24-0.28
Length, externally	0.18(0.18)	0.16(0.18)	0.24	0.18	0.18-0.20
Measured in	Oil of wintergreen		Alcohol		

Olsson spoke of the larva of *T. robustus* being provided with a narrower cylindrical "cauda" as in certain Tetrarhynchus larvae, and gave the length of one as 120mm., while the anterior portion was approximately 60mm. long. Such structures were seen posteriorly in many of the larger larvae at hand but their lengths and degrees of distinction from the fore-body varied considerably. A medium large one, in a lot from *Esox lucius*, for instance, had these measurements: Length of anterior portion, 48mm., of cauda 24, of scolex 1.16; width of forebody 0.66, of cauda 0.37 (3:1—Olsson). The specimen from *Leucichthys artedi* dealt with in the third column of the above table possessed a cauda 110mm. in length, while that treated in the fourth column had no posterior appendage at all. As for its anatomical structure this organ is characterized by very poorly developed cuticula and musculature, and a very loose or open parenchymatous mesh-work.

As may be seen by reference to the host record given below the specimens taken from *Leucichthys artedi* were the only ones belonging to this type of larva which were found encysted. From 26 specimens of the host examined by the writer, 14 cysts, each containing a single larva, were taken. Each fish harbored one or two cysts, but one contained four. The cysts themselves are from 15 to 45mm. in length and 2 to 3mm. in diameter, and cylindrical in shape, with bluntly pointed ends. They are often attentuated at one end to such an extent that at first sight they appear to be terminated by a mere thread. This is found, however, on closer examination to be hollow and to place a more distal, but somewhat smaller portion of the cyst in communication with the main body. In situ these cysts are located constantly in the myocommata of the dorsal musculature of the host, from a short distance back of the dorsal fin to close behind the skull, and with their longitudinal axes directed downward, inward, and forward towards the spinal column, or, indeed as was seen in one case, actually towards the dorsal aorta. Often they are found doubled on themselves in a V-shaped manner. Their translucent white or somewhat opalescent color is due to the contents, which besides the worm coiled on itself several times consists of a caseous substance, showing thru the thin wall.

On the other hand, the other type of larva which is considered by the writer to belong to *T. nodulosus*, is characterized by a much shorter, narrower body, smaller at irregular intervals owing to differences of contraction, whence the specific name, and by a quite different scolex provided with the well-

known form of trident (Figs. 15 to 16). While the latter and the scolex as seen in surficial view agree in essentials with the descriptions and figures given by various authors, e.g., Rudolphi (1810:32, Tab. IX, Figs. 6-11), Wagener (1854: 26, Tab. 2, Figs. 17-21), Olsson (1893:20, Figs. 28-32) and Fuhrmann (1910:86, Fig. 1), it cannot be said of the material studied that, as stated by the last writer, ". . . chez *T. nodulosus* on ne peut voir aucune limite entre le scolex et le cou du Bothriocephale. . . ." For in lateral view (Fig. 16) the bothria are distinctly separated from the beginning of the body, which is, as just mentioned, not nearly so apparent in surficial view. As shown in figure 15, the middle hook of the trident scarcely protrudes thru the cuticula, since it is the root for muscular attachment. The upper median hook (cf. Wagener) which does protrude in the adult is evidently not yet developed (Figs. 17 and 18). For a short distance behind the scolex the body is somewhat rectangular in cross-section, the sides of the rectangle being, however, slightly convex and not concave as in the *robustus* type, and hence not so very different from the cross-section of the body farther back. But the material contained in the lot from the intestine of *Esox masquinongy* does not strictly answer this description since the body just behind the scolex is slightly concave on all sides. Otherwise the specimens are distinctly of the *nodulosus* type. It should be mentioned, too, that one of this lot showed a very short but distinct caudal piece; but this with the general stout appearance of all of them may be accounted for by the possibility that they have reached the intestine of one of their final hosts and continued their development. Likewise a few of the specimens of the lots from the "white bass" and *Stizostedion canadense* were provided with short caudal appendages. The smallest example of this type and of all the material, for that matter, at hand was that from *Micropterus dolomieu* of the accompanying table. Altho it is only a little over two and a half millimeters in length, its posterior end shows that a portion, perhaps a caudal piece, has been torn away. The following table gives measurements of a number of specimens of the *nodulosus* type, similar to those given above for the *robustus* type, with Fuhrmann's data for comparison:

Host	*Catostomus commersonii*	*Esox masquinongy*	*Micropterus dolomieu*		After Fuhrmann
Length	Piece	Piece	Piece	2.68	120-180mm.
Breadth at middle	0.61	0.37	0.42	0.30	2.50-4.00
Length of scolex	0.92	0.63	0.55	0.55	0.95
Width term. disc.	0.42	0.35	0.37	0.31	0.37-0.47
Width of scolex posteriorly	0.64	0.37	0.37	0.26	0.57-0.60
Width of trident	0.19	0.15	0.15	0.13	0.125
Width of trident medially	0.14	0.13	0.11	0.14	0.073
Width of trident externally	1.11	0.09	0.08	0.10	0.062
Measured in	Oil of wintergreen				

It will be noticed that in spite of the fact that all of the measurements of the tridents are larger than those given by Fuhrmann, they are considerably smaller than those of the other type.

Finally, altho no specimens of either type of larva so young that the hooks had not yet developed were met with, those from the intestine of *Stizostedion vitreum* were provided with only very small tridents of the *nodulosus* form, the bases of which were not yet well developed. The whole scolices were a sort of compromise between the two types in shape but of the *nodulosus* type as regards size, as shown in the following measurements: Length, 12mm.; width at middle, 0.64; length of scolex, 0.87; width of terminal disc, 0.64; same of scolex posteriorly, 0.80; width of trident, 0.14, length medially, 0.07, externally, 0.05. Altho these specimens would seem to represent an intermediate stage between the two types of scolex so far as the general shape is concerned, the writer was inclined to consider them as belonging to the *nodulosus* type; yet it must be said that smaller scolices, e.g., those from *M. dolomieu* in the table, have considerably larger hooks.

On the whole, then, the bulk of the evidence given here tends to show that here in America there are probably two species, very closely related to, if not identical with, the European *T. nodulosus* and *T. robustus* which have been clearly distinguished by Fuhrmann (1910) and also recognized by Lühe (1910: 23). However, no adults have as yet been reported for this continent, so far as the writer is aware.

The material studied is here listed as a host record also:

LOT	HOST	LOCATION	LOCALITY	COLLECTOR
Type *robustus*:				
36	*Esox lucius*	Intestine	Flat Rock L. Muskoka, Ont.	Cooper
36a, 36b, 36c	*Esox lucius*	Intestine	Go-Home R., Muskoka, Ont.	Cooper
161, 163, 183,	*Esox lucius*	Intestine	Go-Home Bay,	Cooper
162	*Lota maculosa*	Intestine	Off Giant's Tomb Id., Georgian Bay, Lake Huron	Cooper
15.47	"Lake Herring"	? Intestine	Lake Superior	H. B. Ward
186a, 194b, 195a, 196a, 197a, 25f, 25g	*Leucichthys artedi*	Muscles	Douglas Lake, Michigan	G. R. LaRue
331, 333, 336, 337	*Leucichthys artedi*	Muscles	Douglas Lake, Michigan	Cooper

Type *nodulosus*:	Host	Location	Locality	Collector
71	*Perca flavescens*	In liver	St. Lawrence R., Iroquois, Ont.	Cooper
151, 188	*Micropterus dolomieu*	In viscera	Go-Home Bay	Cooper
195	*Catostomus commersonii*	?	Georgian Bay	Cooper
Eh3b	*Notropis delicatus*	?	Charlevoix, Mich.	H. B. Ward
10213	"White Bass"	Liver	?	H. B. Ward
N. S. 28a	*Stizostedion canadense*	Stomach wall	New Baltimore, Michigan	H. B. Ward
40	*S. vitreum*	Intestine	Flat Rock L.	Cooper
35	*Esox masquinongy*	Intestine	Go-Home R.	Cooper

FISTULICOLA Lühe 1899

Taenia (part.)	Pallas	1781
Bothriocephalus (part.)	Rudolphi	1819
Bothriocephalus (part.)	Leuckart	1819
Bothriocephalus (part.)	Dujardin	1845
Dibothrium (part.)	Diesing	1850
Dibothrium (part.)	Diesing	1863
Bothriocephalus (part.)	Linstow	1878
Bothriocephalus (part.)	Carus	1885
Bothriocephalus (part.)	Matz	1892
Bothriotaenia (part.)	Ariola	1896
Bothriotaenia (part.)	Riggenbach	1896
Fistulicola	Lühe	1899
Bothriotaenia (part.)	Ariola	1900
Fistulicola	Braun	1900
Fistulicola	Lühe	1902

Scolex unarmed, arrow-shaped (since the posterior borders of the surficial bothria protrude comparatively strongly), may be replaced by a pseudoscolex. Neck absent. Chain of proglottides very thick, so that transections may be nearly circular. Segmentation strongly expressed, the individual proglottides very short with leaf-like, free lateral portions. Longitudinal nerves strongly approaching the lateral borders; individual testes, however, are also present outside of them. Pronounced coiling of the vas deferens in its proximal portion; the distal part near the cirrus-sac only weakly coiled. Receptaculum seminis comparatively small and obscure, but at the same time sharply set off from the narrow terminal portion of the vagina (the spermiduct), which in contrast with the Ligulinae, Dibothriocephalinae and Cyathocephalinae is comparatively long. Ovary and shell-gland, near the corresponding parts of the female ducts, are, in consequence of the shortness of the proglottides and the strong development of the uterus, forced away from the position which they usually occupy in the Dibothriocephalidae, or towards the ventral surface or the margin bearing the genital openings. Vitelline follicles extraordinarily numerous, not confined to two lateral fields, but in the form of a ring, outside of the longitudinal musculature in the free lateral leaf-like portions of the proglottides. Uterus a comparatively wide, strongly coiled canal; that portion near its opening very muscular. The eggs pass thru their embryonic development (at least for the most part) in the uterus.

Type species: *F. plicatus* (Rudolphi).

FISTULICOLA PLICATUS (Rudolphi 1819)

1781	*Tacnia haeruca*	Pallas	1781 : 108
1790	*Echinorhynchus xiphiae*	Gmelin	1790 : 3047
1803	*Echinorhynchus xiphiae*	Zeder	1803 : 162
1809	*Echinorhynchus xiphiae*	Rudolphi	1809 : 308
1816	*Echinorhynchus xiphiae*	Lamarck	1816 : 582
1819	*Bothriocephalus plicatus*	Rudolphi	1819 : 136, 470
1819	*Bothriocephalus truncatus*	Leuckart	1819 : 37
1829	*Bothriocephalus plicatus*	Creplin	1829 : 87
1839	*Bothriocephalus plicatus*	Creplin	1839 : 297
1845	*Bothriocephalus plicatus*	Dujardin	1845 : 614
1850	*Dibothrium plicatum*	Diesing	1850 : 591
1854	*Dibothrium plicatum*	Wagener	1854 : 71
1863	*Dibothrium plicatum*	Diesing	1863 : 243
1869	*Bothriocephalus plicatus*	Cobbold	1869 : 71
1871	*Dibothrium plicatum*	Van Beneden	1871 : 36
1878	*Bothriocephalus plicatus*	Linstow	1878 : 218
1885	*Bothriocephalus plicatus*	Carus	1885 : 120
1890	*Dibothrium plicatum*	Linton	1890 : 746
1892	*Bothriocephalus plicatus*	Matz	1892 : 117
1896	*Bothriotaenia plicata*	Ariola	1896
1896	*Bothriotaenia plicata*	Ariola	1896 : 280
1896	*Bothriotaenia plicata*	Riggenbach	1896 : 223
1898	*Dibothrium plicatum*	Linton	1898 : 430
1898	*Bothriocephalus plicatus*	Muehling	1898 : 36
1899	*Fistulicola plicatus*	Lühe	1899 : 37
1899	*Fistulicola plicatus*	Lühe	1899a
1900	*Bothriotaenia plicata*	Ariola	1900 : 437
1900	*Fistulicola plicatus*	Braun	1900 : 1695
1900	*Fistulicola plicatus*	Lühe	1900a : 98
1901	*Dibothrium plicatum*	Linton	1901 : 267
1901	*Dibothrium plicatum*	Linton	1901a: 412, 448
1902	*Fistulicola plicatus*	Lühe	1902a : 321, 324, 329
1903	*Bothriotaenia plicata*	Barbagallo and Drago	1903 : 412
1905	*Fistulicola plicata*	Spengel	1905 : 273
1914	*Fistulicola plicatus*	Rudin	1914 : 321

Specific diagnosis: With the characters of the genus. Large cestodes with maximum length, breadth and thickness of 250 (about 60 when contracted), 20 and 5mm. respectively. Scolex somewhat orbicular, 2mm. long, 1.3 wide and 1.8 thick; present only in young strobilas which are free in the intestine of the host; later it becomes modified as does a considerable portion of the anterior end of the strobila to form a pseudoscolex which is found deeply imbedded in the wall of the host's rectum or completely piercing it. Segmentation begins immediately behind the scolex or pseudoscolex. First and middle segments very short and broad, with prominent posterior and wavy borders; posterior joints 0.4, 7 and 3mm. in length, breadth and thickness respectively, funnel-shaped with prominent posterior borders which occupy two-thirds or more of the transverse diameter; terminal segments relatively much longer, narrower and conical in shape, their posterior margins very thin and leaf-like.

Cuticula 10μ in thickness, subcuticula 50 to 55μ. Calcareous bodies 15 to 25 by 10 to 15μ in dimensions, mostly outside of the longitudinal muscles. Latter not in bundles but distributed thruout the cortical parenchyma, separated into outer and inner groups only in young proglottides. Transverse and sagittal fibres likewise diffuse, former more numerous, however, just outside of the medulla. Chief nerve strand 45μ in diameter, situated far towards the margin of the strobila on each side, passing dorsal to the cirrus-sac and vagina. Excretory system in the form of a plexus of vessels ramifying thruout the whole of the medulla, of which one just within the nerve on each side is small in caliber but provided with thick muscular walls.

No genital cloaca, but the vagina opens immediately behind the cirrus-sac, the outer half of which forms a protruding papilla from 0.4 to 0.6mm. in length and with a marked constriction at its base. Uterus opening about half-way between the median line and the margin bearing the other genital apertures, and on the free posterior portion of the proglottis.

Testes polyhedral in shape; closely arranged, forming a dorsal layer continuous from side to side but discontinuous from proglottis to proglottis; 90 to 130, 55 to 75 and 90 to 185μ, in length, breadth and thickness respectively; quite numerous outside of the nerve strands, at least 200 to each proglottis. Vas deferens strongly coiled and compact in the median line, less coiled laterally; median and distal portions lined with ciliated epithelium; no special enlargement at any point in its course to form a vesicula seminalis. Cirrus-sac 0.5 to 0.7mm. in length by 0.2 to 0.4 in maximum diameter; outer half or more forming the pyriform, protruding cirrus, the cuticula over which is deeply cleft. This functional cirrus may be augmented in length by the further evagination of the cirrus proper from the papillary portion of the organ.

Immediately within its opening the vagina is surrounded by a sphincter, 0.2mm. in diameter, which is followed by a slight enlargement of the lumen to a diameter of 60μ; much coiled laterally but straighter medially; 20μ in diameter at the middle of its course; spermiduct inconspicuous. Ovary irregular in shape, median in position and considerably depressed, 0.7mm. in transverse diameter by 0.1 in thickness, isthmus prominent, ova from same 25μ in maximum diameter. Oocapt 25μ in diameter, oviduct 40μ. Vitelline reservoir 75μ in diameter when filled with vitelline material. Vitelline follicles irregular in shape, very numerous; discontinuous from proglottis to proglottis, but form a continuous layer laterally and dorsoventrally in the free posterior borders of the segments. Shell-gland inconspicuous. Uterus in gravid joints occupies almost the whole of the medulla; 0.16 to 0.20mm. in diameter at its middle; the terminal portion quite muscular, and sharply separated from the duct immediately before it, 0.2 to 0.3mm. in length by 0.10 to 0.15 in diameter; opening irregular in shape and size.

Eggs thick-shelled (2 to 4μ) with dimensions of 0.09 to 0.10 by 0.05 to 0.06mm.

Habitat: In the rectum—less frequently in the stomach and anterior portion of the intestine—of the host.

HOST	LOCALITY	COLLECTOR	AUTHORITY
Xiphias gladius (type host)	Pisa	Redi	Rudolphi 1809 : 309
Xiphias gladius	Baltic Sea	Rudolphi	Rudolphi 1819 : 471
Xiphias gladius	Ticini	Spedalieri	Diesing 1850 : 591
Xiphias gladius	.....	Kais.-König. Nat'l Kab.	Leuckart 1819 : 37
Xiphias gladius	.....	.....	Dujardin 1845 : 614
Xiphias gladius	Gryphswald	Rosenthal	Diesing 1850 : 591
Xiphias gladius	.....	M. C. V.	Diesing 1850 : 591
Xiphias gladius	Lynn, Norfolk, England	Cobbold	Cobbold 1869 : 71
Xiphias gladius	Coast of Norway	Olsson	Beneden 1871 : 36
Xiphias gladius	Escaut	.....	Beneden 1871 : 36
Xiphias gladius	Holland	.....	Beneden 1871 : 36
Xiphias gladius	Firth of Forth, Edinburgh	.....	Beneden 1871 : 36
Xiphias gladius	Nizza	Wagener	Carus 1885 : 120
Xiphias gladius	Martha's Vineyard, Mass.	Linton	Linton 1890 : 750
Xiphias gladius	Genova	Ariola	Ariola 1896a : 121
Xiphias gladius	.....	U. S. National Museum	Linton 1898 : 430
Xiphias gladius	Königsberg	Braun	Muehling 1898 : 36
Xiphias gladius	Siracusa	Condorelli	Ariola 1900 : 438
Xiphias gladius	Naples	Ariola	Ariola 1900 : 438
Xiphias gladius	Casco Bay, Me.	U. S. National Museum	Linton 1901a : 448
Xiphias gladius	Woods Hole, Mass.	Linton	Linton 1901a : 448
Xiphias gladius	Messina, Italy	Barbagallo and Drago	Barbagallo and Drago 1903 : 412
Xiphias gladius	Messina, Italy	Janicki	Rudin 1914 : 321
Xiphias gladius	Woods Hole, Mass.	H. B. Ward	Cooper (the present paper)
"Sunfish" (Mola ?)	Woods Hole, Mass.	V. N. Edwards	Cooper (the present paper)

This species has been so well described by Linton (1890:746), Ariola (1896a) and Lühe (1899a, 1900a) that little need be added. The writer would like to point out, however, that as regards a few details the material studied did not agree with the descriptions given by these writers.

After referring to the fact that the testes are not arranged in two lateral fields but form a continuous dorsal layer and the further fact that, contrary to Ariola's statement, they are to be found evidently functioning in gravid segments, Lühe (1899a:709) stated that "Ihre Anzahl ('pochi' nach Ariola, 'zahlreich' nach Loennberg) beträgt ca. 50 pro Proglottis." In the sections made they were found to be about 200 in number for each proglottis, and separated from those of the segments ahead and behind by aggregations of transverse and sagittal muscles which are, however, so narrow as to give the closely

crowded organs the appearance at first sight of being continuous thruout the strobila.

The vagina was described by Lühe (1900a:68) as being provided with no cuticular lining within the enlargement just beyond the sphincter, but in the sections made by the writer the cuticula could be followed for about half the length of the whole duct. Peripherally as in the case of that lining the terminal enlargements, it was seen to be thrown into prominent longitudinal folds which in transections were in many places fused together so as to divide the lumen into several passages. Farther on these folds become less pronounced and fused, while their borders towards the center of the lumen gradually become broken up into pseudocilia. Beyond the middle of the course of the duct these pseudocilia seem to pass insensibly into the cilia of the proximal region, while the cuticula is likewise strictly continuous with the nucleated epithelium, there being no distinct region, let alone line of demarcation in either case. It would appear, then, that what are apparently true cilia in the proximal portion of the duct are merely modified cuticular pseudocilia; or from the standpoint of development that the latter, as well as the more peripheral ridges, are formed by the gradual fusion of the former from within outwards. But since this view needs considerable ontogenetic evidence for its support, it must remain for the present, at least, a mere suggestion of possibility.

Otherwise the material studied, which was quite fragmentary, corresponded with the descriptions given by the various authors of the species found on the European side of the Atlantic Ocean, as was brought out by Linton (1890) for the general features. It consisted of No. 13.46 of the Collection of the University of Illinois from the stomach wall of *Xiphias gladius*, and one specimen taken by Mr. V. N. Edwards from a "Sunfish" (? *Mola mola*) at the Woods Hole Laboratory of the U. S. Bureau of Fisheries.

PTYCHOBOTHRIIDAE Lühe 1902

Scolex unarmed, with two separate and more or less strongly developed bothria, or exceptionally replaced by a pseudoscolex. Neck absent. External segmentation never absent, but frequently incomplete or obliterated thru secondary foldings. Genital organs numerous, but only single in each proglottis. Both surfaces of the chain of proglottides, apart from the genital openings similar. Cirrus unarmed, with cleft cuticula. Opening of cirrus and vagina behind the uterus opening, surficial or marginal, in the first case on the opposite surface to the uterus-opening and almost median. No muscular bulb at the inner end of the cirrus-sac. Receptaculum seminis, when present, has the form of a small blind sac situated at the inner end of the vagina. Ovary and shell-gland median. Testes in two lateral fields. Uterus never taking the rosette shape, but usually forming a capacious undivided uterus-sac. Eggs thin-shelled, without opercula; embryonic development in the uterus, and in consequence of exhaustive production of eggs (but dependent on the time of year in the case of many species) all the eggs of the whole tapeworm are at the same stage of development.

Sexually mature in the intestine of fishes; larval condition unknown.

In his first diagnosis of the family Lühe (1902a:326) emphasized the similarity of both surfaces of the strobila (in contradistinction to conditions in the Acanthophallidae), the unarmed cirrus with cleft cuticula, the peculiar cecal receptaculum seminis and the absence of opercula in the eggs, but described the uterus as follows: "Uterus nie die sogenannte Rosettenform annehmend, wohl aber in der Regel eine geräumige Uterushöhle bildend, welche die übrigen Genitalorgane, ohne dass freilich deren Rückbildung eintritt, buchstäblich an die Wand drängen kann, indem die ganze Proglottis in reifen Proglottiden vielfach als ein einziger sackförmiger Eibehälter mit verhältnismässig sehr dünnen Wandungen erscheint." The uterus of Haplobothrium answers this description in that it is divided into a uterus-sac and uterine duct; but the remaining reproductive organs are distinctly diphyllobothriidian in their nature. Consequently, in order to differentiate more clearly the two families, Ptychobothriidae and Diphyllobothriidae, and especially since the genus Haplobothrium presents difficulties in this connection, it is necessary to know the developmental relationships between the uterine duct and the uterus-sac in those genera in which they appear. Up to the present no adequate descriptions of the latter have been published, so that here will be given the observations on the development of the uterus to which reference was made above (p. 16), where the conditions in Haplobothrium and Marsipometra were discussed.

In *Bothriocephalus scorpii* the lumen of the uterus-sac appears suddenly and with a diameter of 90μ, the rudiment ahead showing as yet no signs of forming a cavity. This enlargement is situated at first, however, in the cortical parenchyma and among the longitudinal muscles, only the inner tip of the

structure in transections going into the medulla. Just within the inner transverse muscles this inner portion of the sac is joined by the uterine duct which with a diameter of 30μ elsewhere is here only 8μ in diameter. Furthermore, in the genital rudiment of the next proglottis ahead there is a distinct demarcation between the aggregagion of nuclei that will form the sac and the axial rudiment of the uterine duct. The same separation of sac and duct with the narrowing of the latter just before entering the former is present in the following segments even where the first eggs are to be seen in the lumen. Thus the eggs must have passed this narrowed region which is a great deal smaller than their diameters. Still farther back where the lumen is about 165μ in diameter there can be seen not only the situation of the sac in the cortex and among the longitudinal muscles, projecting as yet only a short distance into the medulla—altho here the bundles of muscles are deflected peripherally—but also the separation of the two parts by a narrow neck only 10μ in diameter. *B. cuspidatus* shows the same distinct separation of the uterine duct and uterus-sac in the proglottides where there are already a few eggs in the latter. In *Clestobothrium crassiceps* conditions were found to be quite the same. When the lumen of the sac attains dimensions of about 60 by 35μ and is lined with an epithelium which takes the counterstain more like a cuticula but shows nuclei on its surface towards the lumen, the uterine duct opens into it with a distinct reduction in diameter. The epithelia of the two are, however, quite similar and continuous, the nuclei being located in a similar manner in both. Proglottides ahead show that the sac is formed by an enlargement of the end of the duct, which takes place first in that region passing thru the cortex quite as in Bothriocephalus.

Thus it is seen that the uterus sac of this family is quite different from the functional enlargement of the uterus of the Diphyllobothriidae, with the exception of that of Haplobothrium, since at all stages in its development it is sharply separated from the uterine duct. But as it was not so much this exact separation of the two portions as the constant presence of an "Uterushöhle" in this family and its absence in the other, where the "Rosettenform" is more common, that was emphasized by Lühe, and since the structure in Haplobothrium is distinctly ptychobothriidian in character, the functional enlargement of the uterus cannot now be considered to be of such systematic importance as was formerly believed.

PTYCHOBOTHRIINAE Lühe 1899

Scolex with two surficial sucking grooves, which may be modified by considerable growth together of their free edges. Genital openings surficial, those of the cirrus and vagina dorsal, that of the uterus ventral and ahead of the other two. Vas deferens strongly coiled, dorsal. Ovary ventral; shell-gland dorsal. Vitelline follicles usually in two lateral fields in the cortical or medullary parenchyma. Testes completely filling the medulla, mostly marginal to the longitudinal nerves which are well towards the median line.

Occurrence: Exclusively in fishes.

Type genus: Bothriocephalus (Rud.) Lühe.

The above diagnosis lacks the words "seldom armed" after "scolex" which appear in Lühe's latest (1910:24) characterization not only of this subfamily but of the family, because they do not appear in his earlier papers, (1899:41 and 1902a:336, respectively) nor does there seem to the writer to be any occasion for their use.

BOTHRIOCEPHALUS Rud. 1808, e. p. Lühe 1899, e. p.

Taenia (part.)	Auctorum	
Rhytelminthus (part.)	Zeder	1800
Alyselminthus (part.)	Zeder	1800
Rhytis (part.)	Zeder	1803
Bothriocephalus (part.)	Rudolphi	1809
Bothriocephalus (part.)	Rudolphi	1819
Dibothrius (part.)	Rudolphi	1819
Bothriocephalus (part.)	Leuckart	1819
Bothriocephalus (part.)	Dujardin	1845
Dibothrium (part.)	Diesing	1850
Bothriocephalus (part.)	Baird	1853
Dibothrium (part.)	Molin	1861
Dibothrium (part.)	Diesing	1863
Bothriocephalus (part.)	Carus	1885
Bothriocephalus (part.)	Matz	1892
Bothriocephalus (part.)	Ariola	1896
Bothriocephalus s. str.	Lühe	1899
Bothriocephalus (part.)	Ariola	1900
Bothriocephalus s. str.	Braun	1900
Bothriocephalus s. str.	Lühe	1910

Scolex elongated, with two only weakly developed sucking grooves. External segmentation well developed; between two consecutive genital segments there is always present a saw-tooth notching of the lateral border, yet a corresponding transverse furrow on both surfaces is sometimes lacking. Vitelline follicles in the cortical parenchyma, continuous from proglottis to proglottis, as are the testes. Receptaculum seminis absent. Beginning of the uterus a winding canal (uterine duct) which opens into a large nearly spherical cavity (uterus-sac or uterus s. str.). Uterus opening approximately median, as is the dorsal genital opening.

Type species: *Bothriocephalus scorpii* (Müller 1776)

BOTHRIOCEPHALUS SCORPII (Müller 1776)

[Figs. 21, 22, 55-57, 59-61, 71, 84, 95, 105]

1722	*Vermis multimembris rhombi*	Leeuwenhoek	1722 : 402
1776	*Taenia scorpii*	Müller	1776 : 219
1780	*Taenia scorpii*	Müller	1780 : 179
1780	*Taenia scorpii* (part.)	Fabricius	1780 : 319
1786	*Taenia scorpii*	Batsch	1786 : 235
1788	*Taenia scorpii*	Müller	1788 : 5-6
1788	*Taenia scorpii*	Schrank	1788 : 48
1790	*Taenia scorpii*	Gmelin	1790 : 3078
1799	*Taenia scorpii*	Ratke	1799 : 68
1800	*Alyselminthus bipunctatus*	Zeder	1800 : 236
1802	*Taenia punctata*	Rudolphi	1802 : 109-110
1802	*Taenia scorpii*	Bosc	1802 : 307
1803	*Rhytis bipunctata*	Zeder	1803 : 296
1810	*Bothriocephalus punctatus*	Rudolphi	1810 : 50
1819	*Bothriocephalus punctatus*	Rudolphi	1819 : 138
1819	*Bothriocephalus punctatus*	Leuckart	1819 : 40
1844	*Bothriocephalus punctatus*	Bellingham	1844 : 254
1845	*Bothriocephalus punctatus*	Dujardin	1845 : 617
1850	*Bothriocephalus punctatus*	van Beneden	1850 : 160
1850	*Dibothrium punctatum*	Diesing	1850 : 593
1853	*Bothriocephalus punctatus*	Baird	1853 : 89
1855	*Dibothrium punctatum*	Leidy	1855 : 444
1856	*Dibothrium punctatum*	Leidy	1856 : 46
1858	*Bothriocephalus punctatus*	Cobbold	1858 : 157
1858	*Dibothrium punctatum*	Molin	1858 : 134
1861	*Dibothrium punctatum*	Molin	1861 : 235
1863	*Dibothrium punctatum*	Diesing	1863 : 240
1867	*Bothriocephalus punctatus*	Olsson	1867 : 14, 55
1878	*Bothriocephalus punctatus*	Linstow	1878 : 237
1885	*Bothriocephalus punctatus*	Carus	1885 : 120
1889	*Bothriocephalus punctatus forma bubalidis*	Loennberg	1889 : 32
1890	*Dibothrium punctatum*	Linton	1890 : 731
1891	*Bothriocephalus punctatus*	Loennberg	1891 : 51
1892	*Bothriocephalus punctatus*	Matz	1892 : 105
1893	*Bothriocephalus punctatus forma motellae*	Loennberg	1893 : 13
1893	*Bothriocephalus punctatus*	Olsson	1893 : 16
1898	*Dibothrium punctatum*	Linton	1898 : 430
1899	*Bothriocephalus bipunctatus*	Lühe	1899 : 43
1900	*Bothriocephalus punctatus*	Ariola	1900 : 394
1900	*Bothriocephalus bipunctatus*	Braun	1900 : 1691
1902	*Bothriocephalus bipunctatus*	Fuhrmann	1902 : 446
1902	*Bothriocephalus punctatus forma punctatus vel typica*	Schneider	1902a : 14
1902	*Bothriocephalus punctatus forma rhombi*	Schneider	1902a : 15
1902	*Bothriocephalus punctatus forma cotti-quadricornis* [mihi]	Schneider	1903 : 75
1910	*Bothriocephalus bipunctatus*	Lühe	1910 : 25
1917	*Bothriocephalus scorpii*	Cooper	1917 : 37

Specific diagnosis: With the characters of the genus. Large cestodes, up to 950mm. long by 6mm. wide. Scolex, large, elongate, with prominent

terminal disc, widest anteriorly; length 1.0 to 3.5mm., breadth 0.3 to 0.5. Bothria long and narrow, shallow posteriorly. First segments subcuneate with weakly prominent posterior borders, longer than broad. Middle and posterior segments much depressed, former very short and broad, latter relatively less so and grouped in twos or threes; lateral borders crenulate. Ripe proglottides 2 to 4mm. wide by 0.2 by 0.8 long. Strobila usually incomplete posteriorly.

Cuticula 5μ in thickness. Calcareous bodies 13μ in diameter. Inner longitudinal muscles in fascicles. Six chief longitudinal excretory vessels.

Opening of the genital cloaca at the bottom of a dorsal median longitudinal depression running thruout mature segments, on a low papilla in each proglottis and half-way between the anterior and posterior borders. Vaginal opening immediately behind that of cirrus. Distinct ductus hermaphroditicus present.

Testes subspherical, 35 to 70μ in diameter and 30 to 60 in each segment. Vas deferens a compact mass lateral to cirrus-sac and opposite the uterine tube, 0.18 by 0.10mm. Cirrus-sac at right angles to dorsal surface, 115 by 120 by 75 to 80μ, extending only a short distance into the medulla; thick layer of nuclei within its wall. Cirrus proper, not protruded, 65 by 15μ.

Ovary compact, tubulolobular, 0.33mm. wide by 0.15 long where uterus-sac is not greatly distended. Isthmus only ventral. Oocapt 35μ in diameter. Vitelline follicles in two lateral weakly united fields on each surface, 350 to 540 in number, 35 to 55μ in diameter; vitelline reservoir small. Shell-gland large, 115μ wide by 85μ deep, median, close behind cirrus-sac. Uterine duct voluminous on both sides of the median line, closely applied to ovary behind. Uterus-sac spherical to flattened anteroposteriorly, occupies one-sixth of transverse diameter of proglottis, alternating irregularly from side to side, or often quite median. Opening in middle of sac, ventral and well forward, formed by the rupture of a distinct membrane.

Eggs, 66 to 80μ in length by 43 to 45μ in diameter, without opercula, forming dark brown maculations in ripe proglottides as they show thru the walls of the uterus-sacs.

Habitat: In the intestine of the host.

HOST	LOCALITY	COLLECTOR	AUTHORITY
Cottus scorpius (type host)	Denmark	Müller	Müller 1788 : 6
Cottus scorpius	Gryphswald	Rudolphi	Rudolphi 1819 : 139
Cottus scorpius	Ireland	Bellingham	Bellingham 1844 : 254
Cottus scorpius	"Oresund e Berg," Sweden	Olsson	Olsson 1867 : 55
Cottus scorpius	Norway	Loennberg	Loenberg 1890 : 22
Cottus scorpius	Grafverna and Näset, Sea of Bahusia	Olsson	Olsson 1893 : 16
Cottus scorpius	Arctic Ocean	.....	Linstow 1901 : 281
Cottus scorpius	Gulf of Finland	Schneider	Schneider 1902 : 15

HOST	LOCALITY	COLLECTOR	AUTHORITY	
Cottus scorpius	Murman-Küste	Coll. Zool. Mus. K. Akad. Wiss., Petrograd	Linstow	1903 : 19
Cottus scorpius	White Sea	Danilevskij	Linstow	1903 : 49
Cottus scorpius	North Sea	Nicoll	Nicoll	1907 : 70
Cottus scorpius	Firth of Clyde, Millport, Scotland	Nicoll	Nicoll	1910 : 355
Cottus bubalis	England	Cobbold	Cobbold	1858 : 157
Cottus bubalis	Norway	Loennberg	Loennberg	1890 : 22
Cottus bubalis	Sweden	Loennberg	Loennberg	1891 : 51
Cottus bubalis	Grafverna and Näset	Olsson	Olsson	1893 : 16
Cottus bubalis	North Sea	Nicoll	Nicoll	1907 : 71
Cottus quadricornis	Gulf of Finland	Schneider	Schneider	1903 : 75
Pleuronectes boscius	Naples	Rudolphi	Rudolphi	1819 : 139
Pleuronectes flesus	"Oresund e Berg"	Olsson	Ariola	1900 : 396
Pleuronectes maximus	Denmark	Müller	Müller	1788 : 6
Pleuronectes maximus	Gryphswald	Rudolphi	Rudolphi	1819 : 139
Pleuronectes maximus	Ireland	Bellingham	Bellingham	1844 : 254
Pleuronectes maximus	Langrunne, Rennes	Dujardin	Dujardin	1845 : 618
Pleuronectes rhombus	Naples	Rudolphi	Rudolphi	1819 : 139
Pleuronectes rhombus	Ireland	Drummond	Bellingham	1844 : 254
Pleuronectes solea	.....	Kais.-König. Nat'l Kab.	Leuckart	1819 : 40
Torpedo ocellata	Naples	Rudolphi	Rudolphi	1819 : 139
Torpedo oculata	.....	Volz	Volz	1900 : 55
Gadus aeglifinus	Arctic Ocean	.....	Linstow	1901 : 281
Gadus minutus	Naples	Rudolphi	Rudolphi	1819 : 139
Arnoglossus boscii	Naples	Rudolphi	Ariola	1900 : 396
Arnoglossus pegosa	Ariminus	Rudolphi	Rudolphi	1819 : 139
Arnoglossus solea	.....	Mus. Vienna	Rudolphi	1819 : 139
Trigla adriatica	Hafnia	Eschricht	Diesing	1850 : 594
Trigla lineata	Ireland	Drummond	Diesing	1850 : 594
Psetta maxima	England	Siebold Coll., Brit. Mus.	Baird	1853 : 89
Platessa plana	Pennsylvania	Leidy	Leidy	1855 : 444
Platessa flesus	Germany	.....	Lühe	1910 : 25
Platessa passer	Trieste	.....	Stossich	1898 : 116
Rhombus maximus	Italy	Molin	Molin	1858 : 134
Rhombus maximus	Patavia	Molin	Molin	1861 : 235
Rhombus maximus	"Oresund e Berg"	Olsson	Olsson	1867 : 55
Rhombus maximus	Trieste	Stossich	Carus	1885 : 120
Rhombus maximus	Venice	Ninni	Stossich	1890 : 7
Rhombus maximus	Warnemünde	.....	Matz	1892 : 105
Rhombus maximus	Rossitten, Cranz, Memel	.....	Muehling	1898 : 36
Rhombus maximus	Trieste	.....	Stossich	1898 : 116
Rhombus maximus	Genova	Parona and Ariola	Ariola	1900 : 395
Rhombus maximus	Trieste	Stossich	Stossich	1901 : 97

HOST	LOACLITY	COLLECTOR	AUTHORITY
Rhombus maximus	Gulf of Finland	Schneider	Schneider 1902 : 15
Rhombus maximus	North Sea	Nicoll	Nicoll 1907 : 72
Rhombus barbue	.....	Volz	Volz 1900 : 55
Rhombus laevis	"Oresund e Berg"	Olsson	Olsson 1867 : 55
Rhombus laevis	Grafverna and Näset	Olsson	Olsson 1893 : 16
Rhombus maeoticus	Odessa	Nordmann	Linstow 1901 : 281
Lophopsetta maculata	Martha's Vineyard, Mass.	Linton	Linton 1890 : 732
Bothus maculatus	Woods Hole	Linton	Linton 1898 : 430
Hemitripterus americana	.....	U. S. Nat. Mus.	Linton 1898 : 430
Hemitripterus americana	Casco Bay, Maine	U. S. Nat. Mus.	Linton 1898 : 430
Hemitripterus americana	Woods Hole	U. S. Nat. Mus.	Linton 1898 : 430
Limanda ferruginea	Block Id.	U. S. Fish Com.	Linton 1898 : 430
Limanda ferruginea	Woods Hole	Linton	Linton 1901 : 485
Labrus maculatus	"Oresund e Berg"	Olsson	Ariola 1900 : 396
Motella mustela	.....	Mus. Vienna	Ariola 1900 : 396
Mullus barbatus	Genova	Parona	Ariola 1900 : 396
Solea monochii	.....	Mus. Vienna	Ariola 1900 : 396
Acipenser ruthenus	.....	Volz	Volz 1900 : 55
Scorpaena porcus	.....	Volz	Volz 1900 : 55
Paralichthys oblongus	Woods Hole	Linton	Linton 1901 : 484
Lota vulgaris	Dvina-Fluss	Danilevskij	Linstow 1903 : 19
Raja clavata	Black Sea	Pilat	Pilat 1906 : 191
Anguilla vulgaris	River Dee, Scotland	Scott	Scott 1909 : 79
Decapterus punctatus	Woods Hole Region	.....	Sumner, Osburn and Cole 1913 : 586
Hippoglossus hippoglossus	Woods Hole Region	.....	Sumner, Osburn and Cole 1913 : 586
Myoxocephalus aeneus	Woods Hole Region	.....	Sumner, Osburn and Cole 1913 : 586
Myoxocephalus octodecimspinosus	Woods Hole Region	.....	Sumner, Osburn and Cole 1913 : 586
Palinurichthys perciformis	Woods Hole Region	.....	Sumner, Osburn and Cole 1913 : 586
Paralichthys dentatus	Woods Hole Region	.....	Sumner, Osburn and Cole 1913 : 586
Pseudopleuronectes americanus	Woods Hole Region	.....	Sumner, Osburn and Cole 1913 : 586

HOST	LOCALITY	COLLECTOR	AUTHORITY
Scomber scomber	Woods Hole Region	.....	Sumner, 1913 : 586 Osburn and Cole
Trachurops crumenophthalmus	Woods Region	.....	Sumner, 1913 : 586 Osburn and Cole
Urophycis chuss	Woods Hole Region	.....	Sumner, 1913 : 586 Osburn and Cole
Hemitripterus americanus	Passamaquoddy Bay, New Brunswick	A. R. Cooper	Cooper (the present paper)
Hemitripterus americanus	Brandy Cove, St. Croix R., New Brunswick	A. R. Cooper	Cooper (the present paper)
Hemitripterus americanus	Woods Hole	V. N. Edwards	Cooper (the present paper)
? *Myoxocephalus aeneus*	Woods Hole	V. N. Edwards	Cooper (the present paper)
? *Myoxocephalus groelandicus*	Woods Hole	V. N. Edwards	Cooper (the present paper)

Most of the specimens studied ranged in length from 50 to 240mm., but none of them were considered to be complete posteriorly. The smallest measured 28mm. in length and the largest 677mm. The scolex assumes a variety of forms in preserved material, but agrees in general with the descriptions of that of *B. scorpii* given by all the authors from the time of Rudolphi (1810: 51). Its commonest shape is shown in figures 21 and 22 where it is seen to be quite elongated, somewhat broader and truncated anteriorly and narrow posteriorly. The anterior portion is in reality in the form of a low pyramid, comparable internally as well as externally with the terminal disc of the Triaenophorinae. Its base is deeply indented dorsoventrally, that is opposite the bothria, but rounded laterally. The whole scolex is broadest at about its middle and narrowest at its posterior end. A portion of the latter is here considered to be the beginnings of the first segment on account of its being constantly set off from the rest of the scolex ahead by a more or less definite groove. The bothrium is in the form of an elongated V, being ordinarily widest and deepest just behind the terminal disc and much narrower and shallower posteriorly where it is not bounded by a definite wall but spreads out on the base of the scolex. In many specimens, however, the scolex is so contracted and the walls of the bothrium so protruded that the latter shows its greatest depth at the middle of the scolex. In lateral view (Fig. 22) the scolex is more nearly oval in outline since it is a little wider towards the base. From this fact it is conceivable that Müller's (1788, Fig. 7) showing a more "orbicular" scolex in *B. scorpii* in lateral view may be explained by supposing that he was dealing with a much contracted specimen, altho in justice to the other side of the question, it must be said that the first segments in his figure are by no means contracted. It will be noticed that the figures of the scolex given here agree

very closely with that of Scott (1909, Fig. 3, Pl. V). However, from the fact that he records *B. scorpii* as having been found in *Anguilla vulgaris*, it is quite possible that he had in reality *B. claviceps* (Goeze) which has been found only in eels up to the present, so far as the writer is aware.

Segmentation begins immediately behind the scolex, so that there is no true neck. The base of the scolex, nevertheless, has the appearance of a very short neck region from which the foremost segments are cut off as soon as they form. Such in fact is considered to be the case. The anterior part of the strobila on the other hand serves the purpose of a neck in that it shows a division into subsegments in a manner to be presently described. As regards the habit of the whole strobila and the general shape of the segments, Rudolphi's (1810:51) description of the species is so applicable to this form that it is given verbatim:

"*Collum* nullum. Corpus planum, margine crenato. *Articuli* capiti proximi plerumque longissimi, angustissimi, subcuneati, margine postico untrinque parum exstante, saepe tamen, praesertim post mortem, contracti, ut reliquis vix longiores appareant. Articuli insequentes anticis breviores et sensim latiores; postici subaequales, fere quadrati, ut plurimum latiores quam longi, interdum quasi ex duobus tribusve confusis compositi, satis magni, margine obtusiusculo hinc inde inciso. Articulus ultimus obtusus.

Linea utrinque longitudinalis articulos majores percurrit. Inter utramque faeturae apparatus."

Leidy (1855:444) described the strobila of the *B. scorpii* which he found in *Platesa plana* as follows: "Neck none. Anterior segments cuneate or triangular; posterior ones quadrate; each with an appearance of three subdivisions, with the subsegments having a pair of generative apertures, in the course of a longitudinally depressed dark colored line, passing the length of the body." Cobbold (1858:157) said of individuals from *Cottus bubalis*: "Toward the lower part of the so-called neck, the joints exhibited at the lateral margins indications of division, which became gradually more defined towards the tail." In the same connection Krabbe (1865:37) stated that, according to Eschricht, "Pendant leur développement ultérieur, l'augmentation du nombre des articles n'est pas toujours exclusivement due, comme chez les Taenias, à la formation de nouveaux articles engendrés par la tête, mais chez quelques espèces, telles que les *B. dubius*, *variabilis* et *fasciatus*, [here *B. punctatus* also] elle est encore produite par la division transversale qui s'opère dans les articles déjà formés." Olsson (1867:55) also referred to multiplication of segments by transverse division of older ones. Loennberg (1891:52) denied this statement of Olsson's, but, as pointed out below, the negation is applicable to the posterior mature segments of this form at least, not to the middle segments referred to by the latter. Linton (1890:773) said "Secondary segments appear at about the twelfth segment from the head. These are formed by a division of each segment into two by means of a median transverse line. This is repeated farther back in much the same manner as described under *D. microcephalum*." In this form such subdivision of segments to form daughter segments occurs

all along the strobila from close behind the scolex to well into the region showing the median row of reproductive rudiments, and in such a manner that, in the anterior part of the strobila at least, what is considered to be a primary segment, situated between the most prominent transverse furrows, becomes subdivided into 2, 4, 8, 16 and finally 32 divisions, each of the latter accommodating two reproductive rudiments. But it must be emphasized that this method of formation of new segments is not strictly followed out, since as it passes backward in development, the primary segment does not always contain 64 genital rudiments. In the first place, some secondary or even tertiary transverse furrows become almost as prominent as the primary ones, and secondly, there is at the same time considerable further subdivision not only of the peripheral tissues but especially of the rudiments themselves. Close behind the scolex the primary segments are very short (Fig. 55), the first six to ten being divided only into two subdivisions in strobilae of moderate size, but into three or four subdivisions in the largest chains. Farther back this process of segmentation takes place gradually; but division is usually seen to occur more readily and quickly in the anterior part of the primary segment or of its major subdivisions, i.e., secondary or tertiary, than in its posterior part—occasionally however the reverse being the case. Thus in general there is a sort of dominance of the anterior end of the segment, which one might call a zooid in the sense in which Child uses the word, over its posterior end as regards metamerism. While this method of formation of segments is further obscured by the fact that often one sees intercalated among primary segments, showing these features well, others which seem to lag behind in division and are hence younger, and that in much elongated strobilas it is still more difficult to distinguish between primary and secondary transverse furrows, owing to their being quite smoothed out especially medially, the whole plan is sufficiently clear to warrant its being described with the definiteness here given. Figures 56 and 57 will give a better idea perhaps of the whole method of segmentation than this description. While in figure 55 the primary segments are indicated by asterisks, in figures 56 and 57 the whole drawing is in each case that of a primary segment. Under the heading of the reproductive system below it will be seen that in the mature portion of the strobila the most prominent transverse furrows are described as coming approximately every eighth or sixteenth genital segment. This is due to the fact that the secondary and tertiary furrows, respectively those dividing the primary segments into two then four parts, become quite as pronounced as the primary ones, thus making it very difficult to follow this plan of segmentation beyond the region of differentiation of the genital rudiments.

At least three prominent longitudinal grooves run thruout the median and posterior portions of the strobila on each surface, even cutting thru the posterior borders in many places. Their course is not regular and they are accompanied by numerous other shorter and more irregular grooves, some of which, but not all, are due simply to lateral contraction of the segments.

The following table gives a list of measurements of representative specimens in alcohol:

Total length in mm.	234	173	130	51	677	*233	*180
Length of scolex	1.20	1.07	0.81	1.14	1.11	5.00	0.85
Breadth of terminal disc	0.30	0.33	0.26	0.33	0.28	0.29	0.27
Breadth at middle	0.35	0.32	0.30	0.37	0.31	0.11	0.22
Breadth at base	0.28	0.27	0.24	0.35	0.26	0.11	0.16
Length of first segment	0.14	0.16	0.09	0.18	0.33	1.83	0.44
Length of posterior segment	0.85	0.46	0.35?	0.57	?	0.54?	0.81
Breadth of same	1.83	1.12	0.53?	0.92	?	1.70	0.99
Maximum breadth of strobila	2.50	1.60	1.05	1.57	3.35	2.80	1.51

*Somewhat stretched during fixation.

Since Lönnberg (1891:52) described the cuticula of the species there has been no mention of it in the literature, so far as the writer is aware. It was found to be 5μ in thickness and composed of two layers, the outer of which is about two-fifths of the whole thickness and is made up of rather stout, closely set "cirri" which stain much more readily than does the inner more homogeneous and lighter layer. These cirri seem to lie on a distinct membrane since their proximal (central) ends are all even and distinguishable in some places as dark granules. In sections stained more deeply than those which show the inner layer as a single homogeneous stratum, the latter is divided into two layers, the outer of which is less deeply stained than the inner and about one-half as thick or one-fifth of the thickness of the whole cuticula. The wavy nature of the cuticula and the basement membrane is as described by Lönnberg, but in many places the membrane is separated from the cuticular musculature by a very thin clear space barely distinguishable with high powers. The cuticula covering the scolex is about 4μ thick, the difference between it and that over the proglottides being due to a thinner homogeneous stratum. The outer layer of the cuticula is not modified to form spinelets on the posterior borders of the proglottides, nor on the edges of the terminal disc, as in *C. crassiceps*, but the pseudocilia are somewhat longer and relatively stouter on the scolex and anterior segments than elsewhere.

The subcuticula, from 25 to 30μ in thickness, has the nuclei of its spindle-shaped cells arranged at various levels so that the space between the cuticula and the vitelline follicles is, excepting for its outer one-third, well filled with them (Fig. 84).

The chalk-bodies, described by Lönnberg, were not studied in living material; but spherical spaces which were evidently occupied by them before they were dissolved out by the acetic acid of the fixing agent, were found to be more

numerous, as Lönnberg stated, in the cortical than in the medullary parenchyma. In the scolex, however, they are somewhat more numerous than in the strobila, in both of which locations they attain a diameter of 13μ.

Lönnberg (1891:53) gave a good description of the musculature of the species, while Lühe (1897a:747) referred to that of the posterior border of the proglottis in the discussion of the arrangement of the muscles of the whole order. In addition to corroborating the findings of these authors, it was noticed by the writer that the fibres of the transverse series are mostly confined to the very short regions between the sets of reproductive organs and are most numerous just ahead of the prominent segmental furrows mentioned above, this applying to both the inner and outer lots. Towards the median line each layer of longitudinal muscles is about 35μ in thickness and composed of bundles of various sizes, in which the fibres are very closely arranged. The outer longitudinal muscles, the extension of which into the posterior borders of the segments immediately behind the scolex are only weakly developed, are in the scolex confined almost completely to very thin bands situated close to the cuticular musculature in the edges of the bothria, as described elsewhere by the writer (1914a:92) for *H. globuliforme*.

Lönnberg (1891:54) described the nervous system so well that little needs to be added. The foremost four large branches from the brain complex were not found to be relatively as large as those shown in Lönnberg's Figure 1a, and the commissure appeared to be divided into two, not distinctly separated, frontal strands, the whole depth of which, including the space between them, was not as much as that shown in his Figure 1c. In the strobila the chief nerve strands, each from 15 to 25μ in diameter, are situated towards the ventral side of the medulla and at the junctions of the lateral and median quarters of the latter, as shown in figure 84.

The excretory system of *B. scorpii* was described in detail by Fraipont (1881:8), while Lönnberg (1891:53) added some further notes on its structure, the former, however, working on living material in which the canals are much more readily seen. In good toto preparations the "canaux descendants" may be easily seen in segments showing the reproductive rudiments as well as farther forward. Owing to a mere accident, temporary preparations showing the details of the reticulum of descending canals in great detail were made by the writer with more or less constant success. When some pieces of a strobila were being transferred from synthetic oil of wintergreen to a slide for the preparation of toto mounts by the further addition of xylol-damar, they suddenly became opaque white and remained so for some time after the damar and coverglass had been added. This opacity was found to be due to air having been drawn into the excretory canals not only thru their cut ends but thru the foramina secundaria. But since the superficial reticulum and all the finer canals were filled with air, nothing of the arrangement of the larger canals could be made out until a short time had elapsed, or until the preparation had been heated slightly. Then the air in the smaller canals became replaced by the xylol-damar, and the larger canals stood out as very distinct silver

threads. This sort of preparation is unfortunately not permanent, since after a few minutes all of the canals disappear, excepting the very largest which can still be followed as in ordinary toto mounts. The results of this method of demonstrating the excretory canals are shown in figure 61, a camera lucida drawing made while the canals were disappearing from view. Three of Fraipont's large "canaux descendants" can be seen together with much of the anastomes among them and at least two branches to foramina secundaria. The largest and most median canal has a diameter of 50μ. But contrary to what was stated by Fraipont (1881:9, 11), only six of these main channels were found close to the ventral layer of longitudinal muscles in the medullary parenchyma, and not six for each surface of the strobila. Lönnberg stated, and correctly too, that their number is very variable as is their size and course, the whole forming a complicated reticulum showing the typical "island formation." As regards the termination of the excretory vessels at the posterior end of the strobila, the writer confirms Fraipont's (1881:10) statement that: "Chez un sujet qui a déjà perdu des proglottis, les gros canaux longitudinaux sont rompus au niveau du bord libre posterieur du dernier segment. Les uns communiquent directement avec l'extérieur, les autres ne sont renfermés et se terminent en cul-de-sac." But no cases were met with in the material at hand in which it could be considered that no segments had been lost. Towards the scolex the six vessels gradually come closer and closer together until in the first segments they may appear for short distances in two sets of three each, dorsoventrally situated; but farther on become lost in their anastomoses. Entering the scolex there may be seen four, three, or two main canals, but they cannot be followed as such thru many sections, since they soon break up into the reticulum mentioned by Fraipont as ramifying thruout the scolex.

Of the generative organs the earliest writers were able to discern only the external openings ("oscula") and the uteri which, showing their contained, dark brown eggs thru the body wall as a longitudinal series of dark punctations, gave origin to the specific names of Zeder (1800) and Rudolphi (1802 and 1810). Concerning these characters Müller (1788:6) wrote as follows:

"Margines corporis depressi intersectione articulorum crenati apparent; oscula in anterioribus articulis nulla adsunt, in posterioribus vera altera in pagina *pori* in macula albida nigricantes, in altera *papilla* alba subelevata, punctaque seu globuli utrinque dispalati, qui *ovula*. *Oscula* seu pori non seriem rectam in corpore. Taeniae sed hinc et illinc divergentem constituunt, alterum in centro articuli, alterum in intersectione constituum. Articuli postici reliquis latiores punctis utrinque dispersis medio autem coacervatis papillullamque exhibentibus repleti sunt; horum coacervatio oculo nudo punctum centri nigrum offert, armatus vero ovula seu globulos e membrana ovata pellucida punctulis nigricantibus impleta constantes discernit."

Rudolphi (1810:50) described them in these words:

"Singuli enim articuli in superficie dorsali nodulum orbicularem, simplicem vel duplicem, subelevatum, vel albidum vel fuscescentem aut nigrescentem

exhibent; in superficie autem ventrali nodulus simplex vel duplex, pariter, sed minus, exstans, quasi perforatus videtur; corporeque pellucido nodulis illis linea corporis media, plerumque tamen irregularis oritur. Noduli aperti *ovaria* sistunt, *ovisque* ellipticis mediocribus referti sunt, haec etiam saepe circa eosdem effusa sunt." From these descriptions it is to be seen that while Müller made correct observations concerning the relations between the positions of the genital openings and the transverse furrows mentioned above, Rudolphi considered the ventral surface to be that on which the openings of the cirrus and vagina are situated and the dorsal that on which the uterus opens to the exterior.

Van Beneden (1850) seems to have been the first writer to describe the anatomy, with however some errors of interpretation as pointed out by Lönnberg (1891). After Lönnberg's the best and practically the only description of the genitalia was given by Matz (1892:105), Ariola (1900:394) and Lühe (1910:25) obviously copying in part at least from him.

The earliest traces of the reproductive rudiments appear in toto mounts about 35 to 40mm. from the tip of the scolex. From this region backwards they increase in size, but so slowly that in large strobilas there may be an intervening stretch of at least 225mm. before the genital sinus appears. Then the rudiments differentiate very quickly, the first eggs appearing in the uterus-sac about 2mm. farther on in one toto mount made. In the largest strobila at hand the first genital sinuses were seen, when the worm was examined in alcohol, about 375mm. from the tip of the scolex, and the first traces of eggs showed thru the ventral body wall about 20mm. farther on.

Van Beneden (1850:162) was the first to mention the relations between the external segments and the sets of reproductive organs. He said: "Dans chaque anneau, il y a deux ou trois appareils mâles et femelles complets; je pense que ces anneaux se divisent encore plus tard, de manière à n'avoir plus qu' un appareil dans chaque animal," [here "animal" is evidently a misprint for "anneau"]; and further in his footnote referring to the superscript after "complets": "J'ai vu des anneaux qui en contenaient jusqu'à six." In his figure 4, Pl. XXI, he showed four parts of the strobila containing evidently three or four sets of reproductive organs in each segment, with the latter subdividing so that two sets appeared in each subsegment in the fourth part of the figure. Leidy described the posterior segments of *B. scorpii* as " . . . quadrate; each with an appearance of three subdivisions, with the subsegments having a pair of generative apertures, in the course of a longitudinally depressed, dark colored line, passing the length of the body." Linton (1890:733) referred to "the phenomenon which the posterior segments present of being welded together in groups of three or four, an appearance which is quite characteristic of the posterior segments and which has been alluded to in various descriptions of the species," while further, in connection with the apertures of the reproductive organs: "In the middle of the strobila there sometimes appear to be as many as four or more papillae to a single segment;" and with reference to the specimens from *Lophopsetta maculata*: " . . . toward the

posterior end of the body the adult segments are arranged in groups of from four to six simple segments, as if the latter were partially fused together, which is another characteristic of this species." From these statements and the further fact that the posterior proglottides have been described as trapezoidal (Stossich), quadrate (Rudolphi, Linton), subquadrate (Diesing), or at most, broader than long (Rudolphi)—actually about twice as broad as long from Linton's (1890:732, 734) description—it is evident that the groups of four sets of reproductive organs (much less frequently three, five or six) shown here in figures 59 and 60, and separated from each other by grooves which in alcoholic material appear to be complete, have been considered to constitute the ripe proglottides. But, as pointed out by Lönnberg, the lesser transverse furrows are only "greater wrinkles or foldings of the surface" and do not cut in deep enough to cause the parts immediately ahead to stand out distinctly like the posterior borders of the proglottides of other species, e.g., *C. crassiceps*. Such posterior borders, with their accompanying "complete" transverse furrows, do occur, however, but only at considerable intervals. One case is shown in figure 95, where it will be noticed there is no such distinct separation of the proglottis from the next one ahead. So far as the writer is aware, this has been pointed out only by Lühe (1910:25) who said: " . . . in reifen Gliederstrecken liegen zwischen zwei völlig durchgehenden, aber auch nur wenig hervortretenden oberflächlichen Querfurchen in der Regel 16 sehr kurze Genitalsegmente, die äusserlich voneinander nur durch Zackenbildungen des Seitenrandes gescheiden sind." In this connection it should also be noted that in his description of *Fimbriaria fasciolaris* (Pallas), a taenioid from various water birds, Wolffhügel (1900:94) remarked that it is comparable to *B. scorpii* in that "eine bis ins aussergewöhnliche gestiegerte Anzahl von Geschlechtsapparaten in einer Proglottis sich folge."

In a considerable length of one toto mount of this form there were found ahead of and including the region of differentiation of the reproductive rudiments the following consecutive number (from behind forwards) of genital segments between the most pronounced transverse furrows, that is in the primary segments in question: 67, 82, 101, 107, 90, 111, 116, using as the criterion of a genital segment, especially ahead of the region of differentiation, the aggregation of nuclei in the median line which will go to form the central organs and ducts of the sytem. There is, however, much difficulty in making these counts on account of rudimentary or intercalated groups of nuclei which, judging from conditions to be seen in the region of differentiation, may or may not form complete sets of genitalia, and above all of the further subdivision of many of these rudiments, which otherwise proceeds in quite the same manner (Fig. 57) as that of the external segments in the anterior part of the strobila. Furthermore, there may often be seen either in the anterior part of the region of differentiation or much farther ahead (Fig. 57) a lateral doubling of the developing genitalia. But since no case was met with of two sets of reproductive organs in a ripe genital segment, it was concluded, especially because of the great infrequency of this duplication, that one or the other rudi-

ment eventually gets the upper hand and develops at the expense of the other. This is borne out by the fact that in half the cases one rudiment was much larger than the other. The above mentioned groups of rudiments were divided and subdivided by less and less pronounced transverse furrows in the following manner:

67				82					101						
43		24		35		47			54				47		
24	19	10	14	14	21	18	13	16	16	14	12	12	20	12	15

This continued until eventually the groups of four (or five, rarely six) sets of genitalia of the authors could be made out. Each of these in turn was seen to be divided into two groups of two sets each, so that each lateral crenulation corresponded to two (or three) of them, i.e., to the 1-32nd division described above (Fig. 57). In ripe segments this arrangement may obtain or the segment may divide again peripherally, so that each crenulation then corresponds with one set of genitalia (Figs. 59 and 60). The latter figures show that "complete" transverse furrows are present between every 8 or 9 (sometimes 7, or apparently even 3, 4, 5 or 6!) genital segments. However, other more relaxed strobilas in alcohol showed complete furrows only every 16 to 17 sets of genital segments, there often being a group of 5 instead of the much more common group of four—but in the same neighborhood of the strobila just as complete grooves every 8, 9 or 10 sets. This shows that a grouping of the genital segments into lots of approximately 16, as mentioned by Lühe (1910:25) is so irregular that it can scarcely be said to occur "as a rule," and that the peculiar method of segmentation of the anterior end of the strobila mentioned above (p. 102) is very difficult to follow with any degree of certainty beyond the region of differentiation of the genital rudiments.

The genital sinus is situated on a low papilla (Fig. 59) on the dorsal surface, in the median line and from one-half to two-thirds of the length of the genital segment from its anterior border, while the uterine opening on the ventral surface is located much farther forward, even at the bottom of the groove corresponding to the indentation of the edge of the strobila, separating the crenulations mentioned above. The sinus itself is circular in outline and from 40 to 45μ in diameter by 15 to 20μ in depth. At its bottom the cirrus and vagina open close together, the latter immediately behind the former, thru a secondary sinus or ductus hermaphroditicus, the walls of which are often found protruding thru the opening of the larger vestibule as if to form part of a functional cirrus (Fig. 95).

The testes are arranged in two lateral fields in the medullary parenchyma, as pointed out by Lönnberg, and are continuous from segment to segment, altho they show some tendency towards division interproglottidally. The number was given by Matz (1892:106) as about 76, with their size as 40.8μ, but here it was found to be from 30 to 60, while their size was 35 to 70μ, 60 being the

commonest measurement. The vas deferens, filled with sperms, forms a compact mass of coils about 0.18 by 0.10mm. in size, lying irregularly to the right or left of the uterine duct or slightly behind the sac and immediately alongside the cirrus-sac, as shown in Fig. 71. The ductus ejaculatorius portion of the vas deferens within the cirrus-sac, that is, that part occupying the lowermost one-third of the latter, has a diameter of from 4 to 6μ. The middle stretch of the duct often expands to 13μ, while the distal part, the cirrus proper, has a maximum length of 65μ with a width of 14μ. Matz gave the dimensions of the organ (? the cirrus-sac) as 100 by 50μ. The cuticula lining the cirrus is pseudociliated on its inner (functionally outer) surface, somewhat as is that on the external surface of the worm. The cirrus-sac is located at right angles to the dorsal surface (Fig. 95) and extends only a short distance into the medulla, as compared to other species. It is ovoid in shape, with the narrower end towards the cloaca, and from 115 to 120μ in length by from 75 to 80μ in diameter. Its wall is composed of an inner thick layer of circular muscles and a very thin outer layer, the fibres of which are directed somewhat obliquely, the whole being 8μ in thickness. As pointed out by Lönnberg and shown in figure 95, the organ is peculiar in that its wall is coated both externally and internally with a thick layer of nuclei which are doubtless mostly myoblastic in their nature. An aggregation of nuclei at the lower pole of the sac, surrounding the vas deferens and continuous with the layer of nuclei on the outside of the pouch, are too numerous to be considered as myoblastic nuclei only. They do not seem to be mentioned either by Lönnberg or Matz. Their arrangement would indicate that they are possibly prostatic in their nature, the whole structure having the appearance of a gland. Retractor muscles of the cirrus proper are scarce. This fact, taken in conjunction with the further fact that the wall of the sac is quite thick and powerful, and that Lönnberg saw only a short thick cirrus when protruded, would lend support to the view that the latter is quite small and not very important from a functional standpoint. Concerning copulation in this species Lönnberg said: "Es ist daher wahrscheinlich, dass die normale Befruchtung so vor sich geht, dass das Sperma in den Sinus genitalis hinausgepresst wird, und davon entweder passiv durch die Kontraktion der Sinus genitalis oder aktiv durch eigene Bewegung in die Vagina gelangt. Sowohl die eine als die andere Weise scheint recht möglich zu sein, weil die Mündung der Vagina ganz neben derjenigen des Penis gelegen ist."

The vagina opens into the ductus hermaphroditicus close behind the cirrus. From there it proceeds close along the cirrus-sac to its lower end, and then turns back to pass over the ovarian isthmus and into the generative space. Its diameter is 13μ, while its wall is composed of a cuticula 5μ in thickness and a thin layer of circular muscles. Its cuticula is retained until the point of union with the oviduct is reached, where the lumen narrows down suddenly to one-half the former diameter (Fig. 105). The ovary with a width of 0.35mm. and a length of 0.15mm., is somewhat irregularly "biscuit-shaped" (Fig. 71) and situated close to the posterior border of the segment or protruding slightly into the segment behind. It is composed of short tubular lobules of varying

size. In transections it is seen to be "concave towards the surface bearing the genital openings" owing to the fact that the ventrally situated isthmus is quite narrow and thick and consequently not well separated from the lobular wings which extend thruout the whole dorsoventral diameter of the medulla and also somewhat enfold the former posteriorly in the median line. Ova from the isthmus are 15μ in diameter, while their nuclei and nucleoli average, respectively, 7 and 3μ. The oocapt is quite muscular, and 35μ in diameter. The oviduct proceeds dorsally for a short distance only before it is joined by the vagina at a vestibule into which the oviduct itself opens (Fig. 105) by a narrow slit much as in *C. crassiceps*. The wall of the duct is composed of an epithelium, in which no cell-boundaries could be made out, but provided with cilia directed towards the uterus. The oviduct continues dorsally for a short distance with the same structure and diameter, namely 18μ, to take on the vitelline duct dorsal to the anterior edge of the isthmus. The vitelline follicles are arranged in the cortical parenchyma in two lateral fields (Fig. 84) which are, however, slightly connected with each other dorsally and ventrally in the median line by a few isolated follicles. No large follicle such as that described by Matz in the neighborhood of the ovary was seen in the material studied. The follicles vary somewhat in size, but average 35 to 55μ in diameter, are very closely crowded together—so as to obscure in toto preparations the testes beneath them—and continuous from proglottis to proglottis. The latter fact makes it difficult, if not somewhat unnecessary, to state the number for each genital segment, but using Matz's method of multiplying the average number seen in transections by that seen in sagittal sections (here the average of several segments was taken), the number varies from 350 to 540, or 440 on the average. Matz gave 490 as the number. Two main vitelline ducts proceed from opposite sides of the genital segment and unite in the antero-dorsal portion of the generative space to form a very short common duct which from the amount of yolk it usually contains may act as a vitelline reservoir, altho the same function is shared even to a larger degree by the much coiled and distended proximal portions of the separate ducts. A few cases were met with in which small ducts laden with yolk came from follicles clearly belonging to the genital segment following. This condition is, however, not surprising in view of the continuous arrangement of the follicles themselves. The diameter of the common duct at its point of union with the oviduct is about 8μ. The very voluminous shell-gland is situated dorsal to the ovarian isthmus close behind the cirrus-sac, with a depth of 85μ and width of 115μ. The uterine duct is quite capacious since it is composed of many coils extending thruout the whole depth of the medulla immediately ahead of the ovary. Proximally it is lined with a syncitial epithelium which distally becomes much attenuated. While it is usually situated in the median line it may alternate from right to left as a whole according as the vas deferens does so on the opposite side of the proglottis, the uterus-sac in such cases remaining in the median line. As above noted, the uterus-sacs were called "ovaries" by the early writers. They were seen thru the body wall to be filled with the characteristic dark brown eggs forming dark patches or

punctations, hence the specific names *bipunctata* and *punctata*. In this species the uterus-sacs were described by Rudolphi, Leuckart (1819:41), *et al.*, as arranged in a single row, in a double row, or alternating thruout the strobila. They were likewise found to alternate irregularly from side to side (Fig. 60) (e.g., r, l, l, r, r, l, r, l, l, r, r, l, etc.) or to be more medially situated (l, m, l, m, m, m, m, l, m, r, r, m, l, l, m, m, etc.) but never in two rows, excepting in a very few immature genital segments (Fig. 57), unless the alternating condition in much contracted strobilas is considered as such. While the sac has a diameter of about 0.18mm. when the first eggs appear in its lumen, it may reach a length of 0.35mm. and a transverse diameter of 0.22mm. or about one-sixth of that of the proglottis. The combined uterus-sac and uterine duct may in many cases occupy more than one-third of the width of the segment. The hindermost segments, in which the uterus-sacs may be gorged with eggs to a diameter of 0.65mm., separate from the chain evidently in pairs, the lines of division taking place at the furrows between the larger crenulations mentioned above. No detached proglottides were found free, however, in the intestine of the host, altho Olsson (1867:55) recorded having found such, while Weinland (1858:9) said that, according to Eschricht, the species "which lives in the sculpin of the Baltic (*Cottus scorpius*) throws off its whole chain of joints every year and then sends out a new one from the neck." Like that of the distal portion of the uterine duct the wall of the sac is composed of a much attenuated epithelium from the basement membrane of which the nuclei, separated by wide intervals, project into the lumen like bosses. The uterus-opening is situated ventrally in the middle of the uterus-sac, and with regard to the external segmentation either in the middle of the larger (double) segment or in the groove separating it from the next ahead or behind. Circular in outline and 50μ in diameter, it is surrounded by an area of radiating nuclei, thought by Lönnberg to be possibly of the nature of a gland for the secretion of a material of use in the passage of the eggs to the exterior. The actual opening is formed by the rupture of a membrane guarding the outlet, which has a thickness of from 15 to 30μ, (cf. *C. crassiceps*).

The fresh egg is ellipsoidal in shape, dark brown in color, and measures from 66 to 80μ in length by 43 to 45μ in transverse diameter. The shell was observed to be about 9μ thick in living material and not provided with an operculum. No mature eggs showing the six hooks of the oncosphere were met with in fresh material in the field.

Nothing was discovered regarding the intermediate host or hosts of this species, not even in the way of food-contents, for the stomachs and intestines of the few sea-ravens examined were all found to be empty. Linton (1890:732) gave as the food of *Lophopsetta maculata* and *Limanda ferruginea*, from which he recorded *Dibothrium punctatum* Rud., "several species of Annelids, fragments of Squilla, and several specimens of a species of Margarita." No specimens smaller than about 25mm. in length were obtained. According to Udinsky's abstract, Pilat (1906:191), working on *B. scorpii* from *Raja clavata* of the Black Sea (the only case of the species having been found in a selachian

fish, so far as the writer is aware) established the fact "dass seine Larven in den verschiedenen Fischen oder Tieren, welche von Rochen (*Raja clavata*) gefressen werden, sich befanden."

From the foregoing description it is to be seen that this form is very closely related to the *B. scorpii* (Müller) of Europe, altho in many respects it is so different as to almost warrant the erection of a new species to accommodate it. However, on account of the fact that several forms of the European species have been reported, namely, *B. scorpii forma bubalidis* and *forma motellae* by Lönnberg (1889:32 and 1893:13) and those from *Rhombus maximus* and *Cottus quadricornis* by Schneider (1902a:14 and 1903:75), it is considered that here in America one finds the same species as has been found in Europe. And from a comparison of the measurements given above with those given by Leidy (1855: 444) and Linton (1890:732, 734 and 1897:430), it seems that, little as one can rely on external measurements, they also point to definite differences of habit as this worm is found in different host species on this side of the Atlantic.

In the table given below under *B. claviceps* the important diagnostic data of this form are placed alongside those of the European species for the sake of comparison.

The material studied consisted of lots Nos. 191, 196, 197, 198, 287, and 288 of the writer's collection from the intestine of *Hemitripterus americanus* (Gmelin), No. 17.57 of the Collection of the University of Illinois from the same host, and No. 17.56 of the same collection from *Myoxocephalus aeneus* (?).

DIBOTHRIUM ANGUSTATUM (Rudolphi), species inquirenda

Linton (1901a:454, 474) reported this species from *Poronotus triacanthus*, the butter-fish, and *Merluccius bilinearis*, the silver hake. Regarding specimens from the former he said: "9. *Dibothrium angustatum* Rudolphi. Intestine [Pl. XXIV, figs., 269, a, b, c.]

Thirty-seven young strobiles, August 21, 1899. These agree closely with Diesing's synopsis of this species: 'Head elongate, tetragonal, slender, with oblong lateral bothria; neck very short. First segments elongated, very narrow, succeeding segments shorter, subquadrate.'

The outline of the head varies with the state of contraction, but the prevailing form is linear, oblong or somewhat clavate. Segments slender, almost cylindrical, slightly enlarged at their posterior ends. Dimensions of an alcoholic specimen in millimeters: Length of head, 1.16; breadth, anterior 0.33, greatest breadth 0.33, posterior 0.19. Another: Length of head 1.21, breadth anterior 0.22, greatest breadth 0.26, posterior 0.17. Longest head measured 1.92mm. in length to the first distinct segment. The strobiles are linear or nearly so and measured about 25mm. in length."

The species was originally created by Rudolphi (1819:476) to accommodate two specimens from *Scorpaena scrofa*. The diagnosis he gave, however, applies not only to the anterior end of *B. scorpii* when much elongated, but also to younger specimens of the same. "Ovaria speciei praecedentis [*B. punctatus*—mihi] cui haec etiam valde affinis est," from the same description

strengthens this fact, as does Diesing's (1850:594) remark that *D. angustatum* "speciei praecedentis forsan mera varietas." Dujardin (1845:614) considered the species to be synonymous with Leuckart's (1819:41) *B. affinis* which the latter pointed out was "ähnlich dem *B. punctatus*," only smaller and more elongated. An interesting point that Leuckart brought out, which further strengthens the resemblances to *B. scorpii*, was that "Ein grösseres Glied wechselt gewöhnlich mit einem kleineren ab." "Ovaries" were described as being in one row and nearer the anterior than the posterior edge of the proglottis, which with the general characters of the segments and scolex point to *B. affinis* being merely a variety of *B. scorpii*. Later Diesing (1863:240) added to the diagnosis: "Aperturae genitalium laterales"—that is surficial, and not lateral in the sense of being marginal, as it is now used. Parona (1887:320) gave a description of the external features which differed little from those already published and even with the four figures accompanying it does not permit one to separate the species from *B. scorpii*. Matz (1892:121) merely listed the species, while Blanchard (1894:701) included it in his genus Bothriocephalus. Ariola (1896:263, 272, 280) made a few brief statements regarding the form, in which, besides giving the length and breadth of the strobila as 8.5 to 9cm. and 0.9mm. respectively and the dimensions of the eggs as 70 by 51μ, he said that "'Osservo che esso tanto per le dimensioni del corpo, quanto per i caratteri dello scolice nulla ha di comune col *B. punctatus*, che ha una lunghezza totale di circa 50cm., e quindi constituisce una specie propria, quale appunto l'hanno ritenuta il Rudolphi, il Parona, ed altri elmintologi." He placed the species (p. 280) among those of the genus Bothriocephalus Rud. with dorsoventral bothria, in his classification of the family "Bothriocephalidae s. str." Stossich (1898:116) reported the species from *Scorpaena porcus* at Trieste, but added nothing of diagnostic value, while Ariola (1900:419) continued to hold his former opinions concerning the form: "E con ciò cade il dubbio di Diesing e di Carus, che cioè il *B. angustatus* possa riguardarsi come una varietà del Botriocephalo puntato, il quale ultimo ne è assai lontano, oltre che per notevoli differenze di tutto il corpo, per i botridii dorsoventrali." Linton's report of the species has been referred to; and finally Shipley recognized the species in "Numerous fragments taken from the intestine of the salmon, *Salmo salar*."

Thus it is evident that in the literature there are not sufficient data to enable one to state whether this form is a separate species or not, but much that points to its being only a variety of the quite variable *B. scorpii*. Nor was the writer lead to any conclusions by an examination of the material which Linton (1901:474) described from *Merluccius bilinearis*, contained in No. 6646, U. S. N. M. It was found to be very fragmentary and immature, but on the whole to suggest *B. scorpii* in miniature. A toto preparation of one of the widest pieces showed no traces of the reproductive rudiments, but six chief excretory vessels, arranged quite like those in *B. scorpii*, the median pair being the largest, and all of them quite straight as from pronounced elongation of the whole stretch of segments. On the other hand, the long narrow condition of the scolex seemed to be persistent in the material; but, since no strobilas of *B.*

scorpii nearly so small were at hand for study, the writer cannot say that such characters do not exist in the latter. On the whole it seems best to consider *B. angustatus* a *species inquirenda* until more and better material can be studied and comparisons made between the form that appears here in America and that which is found in Europe.

BOTHRIOCEPHALUS CLAVICEPS (Goeze 1782)

[Figs. 19, 20, 23, 72, 85, 96]

1722	*Vermis multimembris*	Leeuwenhoek	1722 : 490
1780	*Taenia anguillae* (part.)	Müller	1780 : 208
1782	*Taenia claviceps*	Goeze	1782 : 414
1786	*Taenia claviceps*	Batsch	1786 : 211
1786	*Taenia anguillae*	Batsch	1786 : 233
1790	*Taenia anguillae*	Gmelin	1790 : 3078
1790	*Taenia claviceps*	Schrank	1790 : 46
1800	*Rhytelminthus anguillae*	Zeder	1800 : 215
1801	*Taenia claviceps*	Rudolphi	1801 : 103
1802	*Taenia anguillae*	Bosc	1802 : 307
1803	*Rhytis claviceps*	Zeder	1803 : 293
1810	*Bothriocephalus claviceps*	Rudolphi	1810 : 37
1816	*Bothrioc. claviceps*	Lamarck	1816 : 582
1819	*Bothrioc. claviceps*	Rudolphi	1819 : 136, 472
1819	*Bothrioc. claviceps*	Leuckart	1819 : 49
1824	*Bothrioc. claviceps*	Nitzsch	1824 : 97
1844	*Bothrioc. claviceps*	Belilngham	1844 : 251
1845	*Bothrioc claviceps*	Dujardin	1845 : 618
1848	*Bothrioc. claviceps*	Siebold	1848 : 147
1850	*Dibothrium claviceps*	Diesing	1850 : 589
1853	*Bothrioc. claviceps*	Baird	1853 : 89
1854	*Dibothrium claviceps*	Diesing	1854 : 578
1859	*Dibothrium claviceps*	Polonio	1859 : 225
1859	*Dibothrium claviceps*	Molin	1859 : 8
1863	*Dibothrium claviceps*	Diesing	1863 : 241
1867	*Bothrioc. claviceps*	Olsson	1867 : 56
1885	*Bothrioc. claviceps*	Carus	1885 : 120
1892	*Bothrioc. claviceps*	Matz	1892 : 108
1893	*Bothrioc. claviceps*	Olsson	1893 : 16–17
1896	*Bothrioc. claviceps*	Ariola	1896 : 280
1899	*Bothrioc. claviceps*	Lühe	1899 : 43
1900	*Bothrioc. claviceps*	Ariola	1900 : 393
1902	*Bothrioc. claviceps*	Fuhrmann	1902 : 441, 447
1910	*Bothrioc. claviceps*	Lühe	1910 : 25

Specific diagnosis: With the characters of the genus. Large cestodes up to 540mm. long by 2 to 3 wide. Scolex small, elongate, but usually found contracted to an almost spherical shape; 0.5 to 1.5mm. long by 0.3 to 0.5 wide at the middle. Prominent terminal disc. First segments thick, short and crowded; middle, oblong; posterior, or ripe proglottides, usually 2mm. broad by 0.5 to 0.7 long, often quadrate, arranged in groups of two, between which the transverse furrow is not prominent; other transverse furrows well marked.

Cuticula 1 to 2μ thick. Calcareous bodies very scarce. Main longitudinal muscles not in bundles. Four to six chief longitudinal excretory vessels.

No genital papilla; genital cloaca funnel-shaped, midway between anterior and posterior borders of the proglottis. Vagina opens immediately behind the cirrus-sac; no separation between common cloaca and hermaphroditic duct.

Testes large, subspherical, averaging 58μ long, 64 wide and 60 deep; 50 to 60 for each proglottis. Coils of vas deferens loose, close behind uterus-sac, 0.35mm. wide by 0.07 long. Cirrus-pouch ellipsoidal, 127 to 145μ deep by 81 to 104 in diameter, thin-walled.

Ovary compact, 0.45 to 0.55mm. in width, 0.055 in length and 0.18 in depth; isthmus quite thick, ventral. Oocapt 30μ in diameter. Vitelline follicles not separated into two fields on either surface, 450 to 720 in number, 45, 80 and 85μ in length, width and depth, respectively; vitelline reservoir large, 175 by 65μ. Shell-gland posterodorsal, alternating irregularly from right to left opposite the vas deferens. Uterine duct quite voluminous, between ovary and uterus-sac. Uterus-sac transversely elongate, occupying one-third or more of the transverse diameter of the proglottis, usually larger towards the side bearing the opening; openings form a zig-sag ventral row.

Egg, 58 to 63μ long by 37 to 40 wide, without opercula; light in color, show only faintly thru the body-wall.

Habitat: In the pyloric portion of the intestine of the host.

HOST	LOCALITY	COLLECTOR	AUTHORITY	
Anguilla vulgaris	.....	Leeuwenhoek	Diesing	1850 : 590
Anguilla vulgaris	.....	Zeder	Diesing	1850 : 590
Anguilla vulgaris	Rennes	Dujardin	Dujardin	1845 : 618
Anguilla vulgaris	Patavia	Molin	Diesing	1863 : 241
Anguilla vulgaris	Onegasee, Russian Finland	Kessler	Schneider	1902 : 17
Anguilla vulgaris	Sinus Codani; L. Holland, Sweden	Olsson	Olsson	1867 : 56
Anguilla vulgaris	Venice	Ninni	Stossich	1891 : 8
Anguilla vulgaris	Ostsee, Warnemünde and Unterwarnow-Rostock	Braun	Braun	1891 : 55
Anguilla vulgaris	.....	.....	Matz	1892 : 109
Anguilla vulgaris	Genova	Parona	Ariola	1900 : 394
? *Anguilla vulgaris*	Nancy	Prenant	Zschokke	1896 : 818
? *Anguilla vulgaris*	Königsberg and Memel	Muehling	Muehling	1898 : 35
Anguilla vulgaris	Peninsula of Porkala, Finland	Schneider	Schneider	1902 : 15
Anguilla vulgaris	Lake Garda, Italy	Largaiolli	Ariola	1900 : 394
Anguilla acutirostris	Ireland	Bellingham	Bellingham	1844 : 251
Anguilla acutirostris	.....	Siebold, Coll. Brit. Museum	Baird	1853 : 90
Anguilla anguilla	Germany	.....	Lühe	1910 : 25
Anguilla migratoria	.....	Kroyer	Stiles and Hassall	1912 : 124
Muraena anguilla	.....	Borke	Goeze	1782 : 414
Muraena anguilla	Gryphswald	Rudolphi	Rudolphi	1810 : 38
Muraena anguilla	.....	Kais.-königl. nat'l kab.	Leuckart	1819 : 49
Muraena anguilla	Hörja, Scania; Lakes Hälen and Refundsjön, Jemtland, Sweden; Bönan, Gulf Bothnia	Olsson	Olsson	1893 : 16
Muraena cassini	Naples	Rudolphi	Rudolphi	1819 : 472
Anguilla rostrata	Chamcook L., New Brunswick	Cooper	Cooper (the present paper)	
Eupomotis gibbosus	Walnut L., Michigan	H. B. Ward	"	"
Gasterosteus bispinosus	Woods Hole, Mass.	V. N. Edwards	"	"

On account of the fact that, according to Rudolphi (1810:31), Müller (1780:208) ascribed four suckers to his *Taenia anguillae*, we must look to Goeze (1782:414) for the first accurate description of the species. Under the name "Der Kolbenkopf, Taenia *claviceps*" he gave the following diagnosis:

"In den Gedärmen eines Aals (Muraena *Anguilla*), worin sie der Graf von Borke gefunden. Nach dem Berichte dieses genauen Beobachters 4 Fuss lang. So lang hat er ihn noch in keinem Fische bemerkt. Mit der Lupe lassen sich die beiden länglichten Saugwarzen an dem kolbenartigem Kopfe dieses Wurms besser, als unter dem Komposito bemerken. Sie sind deutlicher gegliedert, als die Bandwürmer aus den Hechten. Die Endphalangen mit vielen kleinen Knötigen angefüllt. Dies die Aggregate von Eiern, deren sie im Wasser, worin sie aufbehalten wurden, eine unzähliche Menge von sich gegeben hatten. Die Glieder kann der Wurm kurz und lang machen, wie aus der Zeichnung erhellet. Dieses ist also, wie der Graf hinzusetzt, eine besondere Art von Taenien." Gmelin (1790:3078) retained the specific name, *anguillae*, and described the worm as follows:

"T. capite sessili distincto crassiore, articulis oblongis vage torulosis: osculis duobus in uno latere. . . . Habitat in anguillae intestinis, ad 4 pedes longa, capite anterius truncato, articulis 8 proximis longiore, articulis circiter 600, prioribus subquadratis, latitudine longitudinem duplo, posterioribus orbicularibus: latitudine longitudinem octuplo superante." Rudolphi (1810: 38) gave the diagnosis which has been followed by most of the authors since, excepting as regards the position of the bothria:

"*Caput* polymorphum, articulis aliquot proximis simul sumtis longius, cisque crassius, subtetragonum, sub motu saepe utrinque aequale, subovale, plerumque depressum, postice increscens, anticeque non raro margine tumido, untrinque exstante, terminatum. *Foveae* marginales, sive in latere dextro et sinistro (capitis depressi margine) sitae, oblongae, sub motu variabiles, antice plerumque latiores, mox planiusculae, mox magis profundae. Collum nullum. *Corporis* plani et antrorsum angustissimi articuli varii: primi breves; insequentes longiores, tandem subquadrati, quorum singuli antrorsum angustiores, margine postico tumidiusculo, utrinque exstante; articulis ultimus obtusus. Posteriorum margo lateralis alter media saepe parte foramen distinctum habet. *Ovarium* in eorundem articulorum media parte sacciforme, saepe maculam rubescentem refert" or in more condensed form (1810:37; 1819:136):

"B. capite oblongo, bothriis marginalibus, collo nullo, articulis anterioribus brevissimis, mediis oblongis, reliquis subquadratis, margine postico tumido." F. S. Leuckart (1819:49) was unable to find a scolex shaped like that figured by Goeze, but concerning the material he studied he remarked:

"Der Kopf lang, grossentheils fast viereckt, zuweilen auch ganz keulenförmig; bei einigen vorn mehr abgestumpft und der Rand scharf hervorragend. Einige hatten rund um den Kopf über den Gruben eine schmale Vertiefung. Glieder alle viel breiter als lang, sehr schmal, besonders die vorderen, zusammengezogen. Ovarien habe ich an keinem Examplare wahrnehmen können." While Nitzsch (1824:97) added, erroneously, " . . . die Geschlechtmündungen am Seitenrade," Bellingham (1844:251) merely listed the worm from the eel as above recorded. Dujardin (1845:618) made valuable additions to the descriptions of the species but Diesing (1850:589 and 1863:241), Baird

(1853:89), Olsson (1867:56) and Carus (1885:120) did little more than list the worm in their various works; so that it remained for Matz (1892:108) to give the first comprehensive description of the anatomy, particularly of that of the reproductive organs. Later, apart from reports by various workers of the finding of the species, Olsson (1893:16) noted the infrequent occurrence of the worm in the host, an increase in the number of segments by means of transverse division and the variable form of the scolex; Ariola (1896:268, 272, 273, 280; 1900:393), Lühe (1899:43), Braun (1900:1676) and Fuhrmann (1902: 441, 447) dealt with it from a systematic standpoint; and finally Lühe (1910:25) gave a short diagnosis, mostly after Matz, in placing it in his latest classification of the Pseudophyllidea.

According to Dujardin this species ranges in length from 25 to 540mm. (Zeder), but Lühe (1910:25) gave the length, presumably of average individuals, as from 100 to 200mm. with a breadth of about 2mm. While the specimens from *Anguilla rostrata* examined by the writer were quite small, fragmentary, immature and much elongated, the longest piece, however, not exceeding 20mm., two from *Eupomotis gibbosus*, measured 155mm. in length by 2.9 in maximum breadth, and were much contracted, as indicated in figure 19 of the scolex. The latter, according to the authors, varies in preserved material from an almost spherical shape, as mentioned by Goeze and Leuckart and shown in the latter's Fig. 28, Taf. II, to the much elongate form shown in Matz's Fig. 16, Taf. VIII. The tip of the organ may be protruded, flattened or even replaced by a shallow groove which passes from bothrium to bothrium in the sagittal plane, depending on the degree of contraction or relaxation. These differences are brought out here in figure 23, the latter being more like that of Matz. In either case a slight notch is to be seen on the surficial edges of the terminal disc, while the bothria are deeper immediately behind these than posteriorly where they pass insensibly on to the base of the scolex. The segments have been variously described, but Rudolphi's (1819:136) mention of " . . . articulis anterioribus brevissimis, mediis oblongis, reliquis subquadratis, margine postico tumido" may be considered as indicating their condition in average states of contraction. Matz stated that "Die gleich hinter ihm [the scolex] beginnenden Proglottiden sind, wenn nicht contrahiert, ein Viertel oder ein Fünftel so lang als der Scolex. Die geschlechtsreifen Glieder sind 2mm. breit und ein halb bis drei Viertel mm. lang; man bemerkt an den Gliedern häufig sekundäre Teilung, wie bei *B. punctatus* dadurch wohl bewirkt wird, dass der Rand des vorhergehenden über das nachfolgende Glied sich nicht erhebt, höchstens deutet eine rings herumgehende Furche die Grenze an, wie es auch bei *B. punctatus* der Fall ist;" while Lühe (1910:25) said "Die letzten Proglottiden nahezu quadratisch oder sogar länger wie breit." In the material from *Eupomotis gibbosus* all of the anterior proglottides were found to be much broader than long, on account of the contraction of the strobilae, while those in detached pieces were from four to five times as broad as long, as shown in figure 72. Apart from Matz, Olsson (1893:16) and Lühe (1910:25) have noted secondary division of segments, or as Olsson stated the case, "Hos denna art

framträder mycket tydligt och allmänt en förökning af lederna genom tvärdelning; man finner nästen hvarje led genom en svagt framträdande tvärlinie deladt i två lika led, hvartdera med hanliga och honliga organ, om moderledet haft sådana. Äfven die könlösa leden visa samma förökningssätt," which, however, is what Dujardin observed in 1845 when he said that "On remarque en ontre que souvent les articles sont tellement unis deux à deux, que chaque couple parait n'en faire qu'un seul avec une vide transverse et deux appareils genitaux, l'un devant l'autre." This pairing of the ripe proglottides, also shown here in figure 72, is due to the manner of segmentation which is like that described for *B. scorpii*, only quite regular, since the reproductive rudiments appear relatively farther forward in the strobila and seem to be more stable in development. Concerning this method of increase in the number of segments for this species Lühe (1910:25) said, "Zwei aufeinanderfolgende Genitalsegmente äusserlich häufig nur unvolkommen geschieden, indessen fehlen durchgehende Querfurchen auf den Flächen nie auf so weite Strecken wie bei *B. punctatus*." On account of the great degree of contraction of the only two strobilas provided with scolices at hand, the primary segments were not followed with entire satisfaction very far beyond the scolex, but the first two were seen to be divided into four subsegments each—the first one, shown in figure 19, including the four segments to the * at the side of the figure—with some indication of the next division which would result in eight to the primary segment; the third into eight, and so on. There were indications posteriorly, however, that the primary segment consists of at least 32 genital segments or proglottides, but as in *B. scorpii* the furrows separating sets of 16, 8 and 4 genitalia become almost as prominent as those between the groups of 32, while even those separating pairs are not as faint as Olsson (1893:16) stated and showed in his Fig. I, Tab. II. At all events it should be emphasized that the furrows are more distinct and consequently the proglottides better defined, at least externally, than in *B. scorpii*. In the material studied the segments quickly broaden behind the scolex to 2mm. at a distance of 20mm. from the latter, and then very gradually attain the maximum width. The following table gives the measurements of the three largest specimens at hand:

Length of strobila	155mm.	150mm.	43mm.
Maximum breadth	2.9	2.9	2.0
Length of scolex	0.44	0.46	0.46
Breadth of terminal disc	0.22	0.20	0.22
Breadth at middle	0.28	0.30	0.33
Depth of terminal disc	0.20	0.20	0.20
Depth at middle	0.26	0.20	0.40
Depth posteriorly	0.27	0.27	0.46
Width of ripe joints	2.0		1.6
Length of ripe joints	0.40 to 0.50		0.4 to 0.6

The cuticula, between only 1 and 2μ in thickness, is difficult to distinguish from the finely matted and comparatively dense cuticular musculature. The

subcuticula is from 25 to 40μ deep, and the nuclei of its cells are confined to their central halves. No calcareous bodies were seen in the rather fine-meshed parenchyma, altho according to Braun (1896:1262) such were found by Küchenmeister in this species.

The musculature is comparatively weakly developed. The frontal fibres are fine, scattered thruout the medulla and between the longitudinal fibres; while the same may be said of the sagittal series. The longitudinal fibres are comparatively few and widely separated from each other, and as stated by Matz, "are not arranged in bundles."

The chief nerve strands, about 17μ in diameter, are situated distinctly dorsally in the medulla and between the lateral quarters of the transverse diameter of the segment.

Matz described two main excretory vessels, between which is located the nerve strand, on each side of the body, while Dujardin had previously stated that there were four on each side. In the sections made three were seen to follow a constant course on each side, the nerve strand passing between the more median pair. They are shown in figure 85. The medianmost pair are greatly flattened as they pass close against the uterus-sac somewhat ventrally.

Up to the time when Diesing (1863:241) incorrectly described the genital apertures as marginal and alternating, the only references to the reproductive organs of this species were to the uterus-sacs which, being gorged with eggs in the posterior segments, could be seen thru the thin body-wall in the medial line. Carus (1885:120) failed to correct Diesing's error, so that it remained for Matz (1892:109) to give the first and apparently only adequate description of the genitalia, dealing with, however, only the differences between them and those of *B. scorpii*. The earliest traces of the reproductive rudiments appear about 5mm. from the tip of the scolex while the first eggs in the uterus-sacs come at about 55mm. While the opening of the uterus is well towards the anterior edge of the segment, that of the genital cloaca is midway between the anterior and posterior borders. There is no papilla, the opening being a low funnel-shaped depression in which there is no distinction between the external portion of the cloaca and the hermaphroditic duct.

The number of testes as determined directly is from 50 to 60, while their average lengths, breadths and depths are 52 to 63μ, 58 to 70μ and 58 to 63μ respectively. The similar data as given by Matz are: number, 56, size 36 to 47μ. The vas deferens, about 20μ in diameter, forms a mass of open coils, lateral to the cirrus-pouch and posterior to the uterus-sac, thus occupying the opposite side of the median line from that accommodating the bulk of the uterine tube. The whole mass of coils is about 0.35mm. wide and 0.07 long. Entering the base of the sac with a diameter of 8μ, it gradually enlarges until at the cirrus proper it is twice that size. The proximal end of that portion within the pouch, however, is often found enlarged to form a sort of inner seminal vesicle. The cirrus-sac itself ranges in length from 127 to 145μ and in maximum diameter from 81 to 104. Matz gave the measurements as 109 by 64μ. In comparison with that of *B. scorpii* the wall is quite thin and there

is no dense layer of nuclei just within it, as indicated in figure 96, while the retractor fibres and small amount of parenchyma are quite loosely arranged.

From its opening immediately behind the cirrus-sac, the vagina passes downward and backward among the coils of the uterine duct and joins the oviduct at the dorsal edge of the ovary just a short distance from the oocapt. At the middle of its course it is 15μ in diameter. The ovary is from 0.45 to 0.55mm. wide, about 55μ long and 0.18mm. deep, being thus considerably flattened anteroposteriorly. The spherical ova in the isthmus have an average diameter by 13μ. The oocapt is 30μ in diameter, while the oviduct at the point of union with the vagina is often slightly narrower than the vagina, in fact about 10μ. Large right and left vitelline ducts unite in the median line to form the yolk sac which is 175 by 65μ in size. The vitelline follicles with maximum lengths, widths and depths of 45, 80 and 85μ, respectively, number from 450 to 720, or on the average 570 for each proglottis, as calculated by Matz's method. They are not separated into two fields on each surface but strongly united around the reproductive apertures, unlike the *B. claviceps* of Matz, the two ventral fields of which were only weakly united while the dorsal were strongly so. The shell-gland is posterodorsal and on the other side of the median line from the vas deferens. The uterine duct is so voluminous (Fig. 72) that it crowds the uterus-sac and vas deferens to the other side of the median line. It alternates irregularly from right to left, as do the latter. The sac itself is situated in the anterior half of the proglottis where it is somewhat flattened in the longitudinal direction and constantly occupies one-third of the transverse diameter, as shown in Matz's Fig. 15. The openings, each about 30μ wide, form a zig-zag ventral row, since they are not exactly in the median line but as much as 0.3mm. apart. Apart from being somewhat ragged or villous they are not specially noteworthy.

While the eggs of the European form have been given as from 56 to 60μ in length, they were here found to be from 58 to 63μ long by 37 to 40μ wide when measured in the formol in which the specimens were preserved. They are light in color and so do not show thru the body-wall as in *B. scorpii*.

From the above comparison it will be seen that altho the individuals from *Eupomotis gibbosus* (those from which the data were taken) do not exactly agree with the European species, they are sufficiently close to justify their being considered the same. This was made more certain to the writer by the examination of some fragments of the European form, obtained by Professor Ward from Dr. O. Fuhrmann of Neuchâtel, Switzerland, who took them from *Anguilla vulgaris* in "North Germany." But it should be stated that in the latter material the cirrus-sac and ovary are smaller and the uterus-sac much larger, occupying more than half the diameter of the proglottis in many places; or, the reproductive organs seem to become mature relatively earlier, differences in degree of contraction and relaxation being taken into consideration.

The material studied consisted of No. 289 of the writer's collection from *Anguilla rostrata*, Nos. 17.33 and 16.456 from the collection of the University of Illinois, the former from *Eupomotis gibbosus* and the latter from *Anguilla*

vulgaris (North Germany), and No. 17.54 of the same collection from *Gasterosteus bispinosus*.

The most important data of diagnostic value for the two species, *B. scorpii* and *B. claviceps*, are here given in the form of a table for the sake of comparison:

	B. scorpii		*B. claviceps*	
	European data	*Data by writer*	*European data*	*Data by writer*
Length	35-600mm.	677mm.	90-540mm.	155mm.
Breadth	1-7	3.35	2-3	2.9
Length of scolex	0.9-3.0	1.2	0.5-1.5	0.46
Breadth of scolex	0.3-1.7	0.35	0.5	0.30
Breadth of posterior segments	4.0	1.8	2	2.0
Length of same	0.22	0.35-0.85	0.5-0.75	0.5
Number of genital segments per external segment	16	8 or 16	Less than in *B. scorpii*	See text
Number of longitudinal excretory vessels	6, 8, 12	6	4	6
Number of testes	76	30-60	56	50-60
Diameter of same	40.8μ	35-70μ	36-47μ	60-70μ
Dimensions of cirrus-sac	100x50μ	120x80μ	109x64μ	145x104μ
Number of vitelline follicles	490	350-540	462	450-720
Size of same	30-40μ	35-55μ	.....	.....
Arrangement of same	In 2 separate dorsal fields; 2 ventral fields weakly united	Dorsal fields slightly united; 2 ventral fields weakly united	Dorsal fields united; ventral fields weakly united	Dorsals united; ventrals united to same degree
Dimensions of eggs	50-80x40μ	66-80x43-45μ	50-60μ	58-63x37-40μ
Arrangement of uteri	1 row, alternating, or 2 rows	1 row, alternating, or 2rows	.....	.....
Diameter uterus : diam. segment	Only small portion of diameter	1 : 6	1 : 3 - 1 : 2	1 : 3
Longitudinal muscles	Close together	In bundles	Not in bundles	Not in bundles

BOTHRIOCEPHALUS CUSPIDATUS Cooper 1917

[Figs. 24, 25, 69, 70, 86, 102, 106, 107]

1917 *Bothriocephalus cuspidatus* Cooper 1917 : 37

Specific diagnosis: With the characters of the genus. Medium sized cestodes up to 180mm. in length by 2.75 in breadth. Scolex large with very prominent terminal disc deeply notched surficially; bothria long and narrow and quite deep posteriorly giving the scolex when viewed laterally the appearance of an arrow-head; 3.3mm. long, 1.0 wide at middle, 2.5 deep posteriorly. First segments subcuneate and circular in transection, with prominent posterior borders; middle gradually broaden until much wider than long; posterior two to four and half times wider than long, or 1 to 2.7mm. in width by 0.8 in length. Posterior end of strobila usually rounded, even when segments have already become detached.

Cuticula 3.5μ thick, subcuticula 58μ. No calcareous bodies. Longitudinal muscles not in bundles. Four main longitudinal excretory vessels.

Genital cloaca median, halfway between anterior and posterior borders of proglottis, deep and funnel-shaped. Vaginal opening close behind that of cirrus; hermaphroditic duct obscure.

Testes on each side separated into two fields by the nerve strand, inner much narrower than outer; 50 to 60 in each proglottis; 110, 60 and 80μ in maximum width, length and depth respectively. Vas deferens a large compact mass of coils, elongate and lateral to cirrus-pouch, 0.22mm. long by 0.16 in width, alternates irregularly from right to left. Cirrus-sac very large and thin-walled, 0.25mm. in length (depth) by about 0.20 in diameter. Cirrus protruded, 135μ long by 85 in diameter.

Ovary compact, with limbs often turned forward, 0.60mm. wide, 0.10 long and 0.13 thick; isthmus thick. Oocapt 20 to 25μ in diameter. Vitelline follicles 800 to 1000; 70, 50 and 45μ in maximum depth, width and length, respectively; occupying almost the whole of the cortex, strongly united dorsally and ventrally. Common vitelline duct long and narrow. Uterine duct confined to one side of the median line, opposite the cirrus-sac, alternating irregularly from side to side. Uterus-sac spherical, occupying one-third of the diameter of the proglottis; opening median, close to the anterior edge of the latter.

Eggs ellipsoidal, 62 to 66μ long by 42 to 45 wide, oncospheres not developed within uteri.

Habitat: Ceca and intestine of the host.

HOST	LOCALITY	COLLECTOR	AUTHORITY
Stizostedion vitreum (type host)	Flat Rock L., Muskoka, Ont.	A. R. Cooper	Cooper (the present paper)
Stizostedion vitreum	Giant's Tomb Id., Georgian Bay	A. R. Cooper	"
Stizostedion vitreum	Sandusky, Ohio	H. J. VanCleave	"
Stizostedion vitreum	New Baltimore, Mich.	H. B. Ward	"
Stizostedion vitreum	Port Clinton, Ohio	H. B. Ward	"
Stizostedion vitreum	Put-in Bay, Ohio	H. B. Ward	"
Stizostedion canadense	New Baltimore, Mich.	H. B. Ward	"
Stizostedion canadense	Kansas City, Mo.	H. M. Benedict	"
Hiodon tergisus	Havana, Ill.	H. J. VanCleave	"
Hiodon alosoides	Keokuk, Iowa	H. B. Ward	"
"Pickerel"	Gillett Grove, Iowa	G. R. LaRue	"
Percina caprodes	Douglas Lake, Mich.	G. R. LaRue	"
Perca flavescens	Lakes Kegonsa and Monona, Wis.	A. S. Pearse	"

Type specimen: No. 174.2 of the writer's collection.

Co-type: No. 174.3 of the same collection, deposited in the collection of the University of Illinois.

Type locality: Georgian Bay, Lake Huron, off Giant's Tomb Island.

So far as the writer has been able to ascertain a description of this species has not yet been published, nor have any bothriocephalid cestodes been reported for *Stizostedion vitreum* (Mitchill), the common pickerel or wall-eyed pike.

In general appearance this species does not arrest attention until a fairly close examination is made, since it is comparatively small and when much relaxed not so very different, at least posteriorly, from some of the species of Proteocephalus, one of which evidently not yet reported, was found associated with it in the same host. It is medium sized, attaining a length of about 180 mm. with a maximum breadth of about 2.75mm.

The scolex, on account of its comparatively great depth, is more often seen and much more conspicuous from a lateral view (Fig. 25). Dorsoventrally (Fig. 24) it is long and narrow, showing a terminal disc well set off from the bothria, while laterally it is roughly shaped like an arrow-head, as indicated by the specific name chosen, or somewhat comparable to a flask or vase provided with a low conical lid (the terminal disc). The bothria are long, narrow

and elongate oval in lateral view, the greatest depth being near the posterior end. They are separated by a prominent lateral groove on each side, which extends from the anterior edge of the first segment to a dorsoventral groove just behind the disc. The latter itself is deeply notched dorsally and ventrally and on account of this groove quite prominent laterally. It is thus seen that the walls of the bothria are comparatively thin. During life they are quite mobile, as might be concluded from their general appearance as well as from their anatomy. Altho the greatest dorsoventral diameter of both the cavity and the walls is in the posterior portion of the bothrium, the more functional portion would seem to be the anterior part immediately behind the notch of the terminal disc. On account of its powerful musculature the disc evidently greatly assists the relatively thicker walls of the bothria in that region in forming a more powerful organ of adhesion than posteriorly. The thin walls behind would, on the other hand, better assist the sagittal musculature in maintaining suction by presenting a greater surface internally for application to the mucosa of the host's intestine. The measurements of the organ are given in the table below.

The first segments are subcuneate in outline, and show subdivision in a manner similar to that of *B. scorpii*. Each primary segment is divided into two segments of the second order (Fig. 24), and farther back these in turn into segments of the third order, and so on, until in the region where the reproductive rudiments appear the primary segment contains thirty-two subsegments. This plan can be followed as in *B. scorpii* even into the region of differentiation, and indeed much more readily since there is much less irregularity due to intercalated segments and the further subdivision of others. Furthermore, the same sort of dominance of the anterior end of the primary, secondary, tertiary and quaternary segments—that is, until a group of four reproductive rudiments can be recognized—is seen not only in the size of the subdivisions but especially in the first portion of the region of differentiation, in the rate of differentiation of the common rudiment into the different proximal organs of the reproductive system. As soon, however, as the lumina of the uterus-sacs appear, the plan becomes obscured by the gradual enlargement of the posterior borders of the subsegments, even to those of the fifth order. Thus, in turn there may be seen defined, as one follows them backward, groupings of thirty-two, sixteen, eight, four and two sets of genitalia. Eventually, at the posterior end of medium sized strobilas and for considerable stretches of the largest these pairs become separated, so that the segment contains only one set of reproductive organs. These hindermost segments are usually about four and a half times as broad as long, but in the most relaxed strobilas they may be only twice as broad as long. The ripe segments in some cases may be so much elongated and constricted at their ends that they appear barrel-shaped. This accounts for the apparent discrepancy in the measurements of the third and fourth specimens of the table below. As shown (Figs. 25, 69) the anterior part of the strobila has a dorsoventral diameter almost as great as the transverse one—as a matter of fact some parts of the segments are here almost spherical in cross-section—while the

posterior part is comparatively thick and slightly more convex ventrally than dorsally. The strobila as a whole gradually enlarges from the former to the latter.

The following table gives the measurements of six of the largest specimens at hand; all dimensions are given in millimeters.

Length	178	97	66	53	48	38
Maximum breadth	2.74	1.67	1.18	0.72	1.75	1.77
Breadth half way along the strobila	2.04	1.25	0.80	0.64	0.55	1.34
Same immediately behind scolex	0.80	0.26	0.18	0.18	0.18	0.18
Length of scolex	3.35	0.68	1.38	0.83	1.11	1.30
Width posteriorly	0.91	0.26	0.40	0.24	0.37	0.37
Width of terminal disc	1.37	0.31	0.42	0.50	0.44	0.48
Depth posteriorly	2.44	0.27	0.78	0.38	0.60	0.71
Depth of terminal disc	1.16	0.22	0.18	0.26	0.30	0.31
Length of first (primary) segment	1.52	0.15	0.27?	0.14	0.31	0.26
Breadth of same posteriorly	1.03	0.22	0.37?	0.27	0.33	0.31
Length of ripe segment	0.80	0.87	1.14	1.30	0.40	0.61
Breadth of same	2.74	1.67	0.80	0.66	0.51	1.34

The cuticula is very thin, being only 3.5μ in thickness, and with the highest magnifications is resolved into two layers—an outer and an inner, the former about one-half the thickness of the latter, and separated from it by a stratum of granules so minute as to more nearly resemble a membrane. The outer surface of the cuticula is provided with a similar membrane, since there are no cirri or pseudocilia whatsoever. A distinct, tho very thin basement membrane, is also to be seen. The two strata of the cuticula seem to be of pretty much the same consistency since they stain about the same, altho the outer constantly appears somewhat darker at first sight on account of the proximity of its two bounding membranes. On the scolex the outer layer is modified into extremely short and fine spinelets, which, while absent from the terminal disc as well as the posterior borders of the segments, are well developed in the bothria and out over the edges of its walls.

The subcuticula has the usual reticular appearance, is about 58μ in thickness and is provided with numerous comparatively large nuclei (5 to 7.5μ in diameter) distributed equally thruout the tissue, excepting for a stratum about 15μ in thickness immediately beneath the cuticula, which is almost constantly free of them. This outer layer is, of course, composed of the processes of the

syncitial cells below, as well as of other structures lying more deeply in the parenchyma.

The parenchyma shows nothing of particular interest excepting for the comparatively large nuclei of its cells. These are on the average slightly larger than those of the subcuticula, the largest being more constantly about 7.5μ in length. No distinct traces of chalk-bodies were found in sectioned material altho numerous branches of the excretory system resemble such when cut transversely.

The musculature of this species is especially well developed. The frontal fibres, altho rather small, are quite numerous, considerably isolated from each other, and extend from the layer of vitelline glands on one surface to that on the other, everywhere intermingling with the powerful longitudinal series and being discontinuous only where the largest of the reproductive organs are situated. This applies, however, to mature proglottides, for in the segments immediately behind the scolex they are all but absent. In frontal series they are seen to be continuous from segment to segment but naturally slightly more numerous between the sets of reproductive organs, altho they pass freely among the testes. The same description applies relatively to the sagittal fibres. Dorsoventrally they intermingle with the vitelline follicles. On the other hand, the longitudinal series presents quite a marked difference. As a matter of fact the pronounced development of these fibres seems to be an important characteristic of the species. They form an area on each surface in cross-section about 125μ in thickness and consequently so wide as to restrict the cortical and medullary portions of the parenchyma to two narrow regions, respectively about 75 and 90μ in thickness, as shown in figure 86. The individual fibres are large (as much as 6.5μ in diameter), not united into groups as in *B. scorpii* and continuous as a whole from joint to joint. On account of their great number and matted appearance in frontal or sagittal series it was found impossible to determine their exact length; but it may be said that in all probability they do not extend individually for more than one or at most two sets of genitalia along the strobila. Only a weakly developed outer longitudinal series is present, altho the foremost segments have prominent posterior borders, as shown in figure 24. What might at first glance be considered as such, are the very large and numerous longitudinal cuticular fibres forming a comparatively wide area outside of the subcuticular nuclei in the anterior end of the strobila (Fig. 69).

As might be expected from the external appearance of the structure the musculature of the scolex is well developed. Powerful sagittal and radial fibres pass for a short distance behind the terminal disc, which region is therefore, as noted above, the most functional portion of the bothrium. At the middle of the scolex, however, only the sagittal series is very prominent, while posteriorly at the thickest part of the organ, these too disappear almost entirely. The same diminution of the coronal series from in front backwarks is to be seen, although they are at no level nearly so prominent as the other two sets. As in the strobila the longitudinal fibres are very numerous. They pass uninter-

ruptedly into the base of the scolex as two narrow and very thick, dorso-ventral bundles, somewhat trapezoidal in cross-section, and attach for the most part as far forward as the terminal disc to the walls of the bothria in the usual oblique manner. Only a very few pass on to the tip of the scolex. As might be gathered from the prominence of the edges of the terminal disc, its longitudinal arcuate fibres are also very well developed, and obviously essentially related to the greater power of adhesion of the anterior part of the bothrium on each face of the scolex.

The nervous system consists of two chief strands, from 30 to 35μ in diameter, passing thruout the strobila at the junctions of the lateral three-fourteenths with the median four-sevenths of its transverse diameter. These proportions are, however, in other parts of the strobila (especially anteriorly), or in different strobilae, depending on the degree of contraction, often more nearly 1:3:1. They are moreover usually nearer the dorsal surface of the medulla than the ventral. This is on account of the fact that their course is much interfered with by the testes, both having only a limited space in which to accommodate themselves. They pass into the scolex close together—their axes actually about 70μ apart—and then very gradually diverge, only to start to converge again about two-fifths of the length of the scolex from its tip. After diminishing very slightly in diameter each enlarges into an anteriorly truncated ganglion, united with its fellow of the other side by a single commissure which is bent slightly forward into the tip of the terminal disc. The anterolateral edges of the ganglia are at once split into two comparatively large nerves which pass out directly to the edges of the disc and at right angles to the longitudinal axes of the chief strands. This arrangement gives these anterior connections of the nerve strands a very characteristic appearance both in transverse and frontal sections.

The main longitudinal channels of the excretory system are at least four in number, only two of which, however, are at all constant in course, if not in size. These occupy a ventral position thruout the strobila, while the remaining vessels, two or more in number and connected by numerous and irregular branches, are more dorsal in position. In the foremost segments the ventral vessels are comparatively close together and situated considerably within the nerve strands, i.e., towards the median line (Fig. 69). There they vary from 13 to 15μ in diameter, the dorsal vessels having diameters as much as 18μ. As all of these main vessels pass backwards in the strobila they diverge considerably, and become more and more irregular in course as the reproductive rudiments are neared. The ventral vessels, however, remain more constant in course. In the anterior part of the proglottis they pass just outside of the vas deferens on one side and the uterine duct on the other, while in the posterior region of the genital segment they skirt the edges of the ovary or in many cases pass beneath them. They may attain a diameter of 40μ. Furthermore, while the dorsal vessels are forming a very open plexus by numerous large transverse connections in the lateral portions of the medulla, the ventral pair give off at right angles to their courses many short lateral branches passing among the

testes and other median connections more numerous between the sets of reproductive rudiments. In mature proglottides only the more regular ventral vessels can be followed with any degree of satisfaction. As the vessels enter the scolex, the dorsal series soon breaks up into an irregular plexus, consisting of large branches and lacunae, situated more particularly in the large posterior portions of the organ; while the ventral pair quickly diminish in size and regularity of course, but do not lose their identity entirely until at least one-half the length of the bothria is passed. In the youngest strobilas at hand what was considered to be the "end proglottis" showed the excretory system as terminating in an irregular plexus from which numerous foramina secundaria passed to the exterior quite as in Fraipont's (1881, Fig. 8, Pl. II) view of the conditions in *B. scorpii*.

The genitalia have the general habit of the genus. The common genital opening or cloaca, situated dorsally in the median line, is usually about half way between the anterior and posterior borders of the proglottis, while the uterus opening on the ventral surface is quite near the anterior border, so close in fact that in much contracted strobilas it may be all but obscured by the posterior border of the proglottis ahead. Unlike *B. scorpii* both openings are situated at the bottom of comparatively deep depressions, as shown in figure 102, that of the genital cloaca being usually circular in outline, about 0.10 mm. in diameter and 0.11 in depth. In some proglottides, however, it may be so contracted longitudinally as to present a transverse diameter of 0.45mm., with a length of only 0.04 and a depth of 0.13. The ductus hermaphroditicus or secondary cloaca is very shallow in this species, and only about 55μ in diameter. In most of the preparations made it was usually occupied by the tip of the cirrus, when the latter was not extruded, the opening of the vagina forming a very narrow crescent-shaped slit close behind it. In some cases, however, both the cloaca and the ductus were so contracted longitudinally that the tip of the cirrus was found almost inserted into the entrance to the vagina. From this fact, together with the comparatively great depth of the cloaca in such states of contraction, it is conceivable that self-impregnation may take place; but nothing in the nature of a cloacal sphincter to assist in this function is present.

The testes are continuous from proglottis to proglottis in two lateral fields separated by the median row of proximal organs of the reproductive system. Since dorsoventrally they occupy almost the whole diameter of the medulla, each is further separated into two more or less irregular fields by the nerve strand. The more median field consists of little more than one longitudinal row of the follicles. The number of testes is usually from 25 to 30 on each side, with a variation of a few in either direction, thus making the total number from 50 to 60 on the average. They are ellipsoidal in shape with their longest axes transverse to that of the strobila, and attain dimensions of 0.110mm. in width (in the transverse direction), 0.060 in length and 0.080 in depth. On account of their large size, as compared with that of *B. scorpii*, they are naturally much more regularly arranged in the proglottis.

The vas deferens forms a very compact mass of coils lateral to the cirrus-sac and extending from the uterus-sac ahead to the wing of the ovary on that side behind. It alternates irregularly from right to left, as does the greater part of the uterine tube which occupies a similar position on the other side of the cirrus-sac. In states of moderate contraction of the proglottis it is about 0.22mm. in length, 0.16 in width and 0.18 in depth. Immediately within the cirrus-sac the vas deferens continues as a thin-walled seminal reservoir, slightly coiled and occupying approximately the ventral one-third of the former. It varies from 35 to 80μ in diameter, but in the sections made it was found to contain only a comparatively small number of spermatozoa. Beyond this receptacle the duct narrows down to about 5μ in diameter and continues as the ductus ejaculatorius with many coils, situated in the proximal one-third of the sac alongside the seminal reservoir even when the cirrus is protruded. This portion of the duct very gradually enlarges as its circular muscle fibres become more numerous and its lining thicker and thicker as it merges into the cuticula of the cirrus proper. The latter is about 5μ in thickness and deeply "cleft," or, to be more precise, broken up into a great number of coral-like villi by means of irregular separate pittings reaching almost to the base of the tissue. The duct may here (at the middle of the cirrus-sac) attain a diameter of 25μ. The cirrus proper is somewhat conical when protruded (Fig. 102) and has a maximum length and width of 130 and 85μ, respectively. However, on account of the similar structure and large diameter (25μ) of that part of the duct still invaginated within the sac one is led to think that the organ may reach a much greater length—with probably a considerably smaller diameter. From the tip of the cirrus to the inner end of its duct, where the cleft cuticula stops and which point might well be the functional tip of the organ, it is at least 0.28mm. in length. Thus it would seem that the organ functions as a very efficient and powerful intromittent organ. The cirrus-sac is ovoid in shape and comparatively large, being about 250μ in depth (length of longitudinal axis, which is directed dorsoventrally), 180μ in length and 210 in width, when the cirrus is not protruded, and thus somewhat flattened in the longitudinal axis of the strobila. Its wall is only about 2.5μ in thickness, and composed of very fine muscular fibres the direction of which was not determined with certainty. The contents of the sac consists of a loose parenchymatous tissue, containing many nuclei and numerous retractor muscle fibres. The nuclei, which are situated close around the duct and are comparatively numerous, are in all probability myoblastic in their nature. The retractor fibres pass obliquely upwards and inwards from all points of the wall to their points of attachment to the cuticula of the cirrus. This attachment is seen very nicely when the cirrus is protruded (Fig. 102), for then the fibres are much elongated and theycan be followed even to the evaginated cuticula. Their myoblastic nuclei are quite easily distinguished, especially in the everted portion of the cirrus. The cirrus-sacs are all in the median line, their longitudinal axes being almost constantly in the median sagittal plane.

The vagina opens immediately behind the cirrus at the bottom of the genital cloaca with an aperture which forms an arc of a circle. It passes ventrally in the median line close to the posterior wall of the cirrus-sac and then, after taking a few coils on a level with the lower border of the isthmus, it joins the oviduct a short distance from the origin of the latter. Thruout its course it is considerably flattened anteroposteriorly, its dimensions being alongside the cirrus-sac about 46 by 18μ. It is provided with a cuticula, 3μ in thickness and thrown into longitudinal folds. It gradually diminishes in size until a diameter of about 15μ is reached—at the ventral border of the ovary—and then enlarges somewhat before joining the oviduct in a dorsoventral transverse plane, but without forming a distinct receptaculum seminis, altho a considerable length of this portion of the duct is often found filled with spermatozoa. Unlike that of *B. scorpii* the ovary of this species is a compact organ, 0.60mm. wide, 0.10 long (the wings) and 0.13 deep. The elongated oval shaped wings (Fig. 86), usually directed forwards, since the whole organ is situated right at the posterior border of the proglottis and close against the uterus-sac of the next proglottis, are attached by narrow necks to the somewhat wider and bulbous isthmus. Ova from the latter are oval in shape, measure about 15 by 12μ and have nuclei 6μ in diameter with nucleoli 2.5μ. As in *B. scorpii* the wings occupy the whole of the dorsoventral diameter of the medulla, while the median bulbous portion of the isthmus almost reaches the same level dorsally. The oviduct arises dorsolaterally from the isthmus in the somewhat elongated oocapt which has a diameter of 20 to 25μ and a length of from 25 to 30μ. Immediately beyond the oocapt it gradually enlarges from a diameter of 7 to 20μ where it is joined by the vagina only a short distance either to the right or left from its point of origin. At the junction of these two ducts there is only a very small vestibule, as in the foregoing species, into which, nevertheless, the oviduct may be seen to open by a longitudinal slit, and from one corner of which it proceeds with a diameter of 6.5μ. After continuing almost directly dorsally with only a few very open coils it is joined at about the level of the upper edge of the isthmus by the common vitelline duct. Thruout its course the epithelium of the oviduct is poorly provided with cilia and is surrounded by only a comparatively small number of circular muscle fibres. The common vitelline duct has a diameter just beyond its point of origin with the oviduct of 25μ or more. It is directed transversely above the generative space from the dorsal edge of one horn of the ovary to about the median line, where the separate vitelline ducts unite. In sections it is usually filled with yolk cells. The vitelline ducts, themselves, pass laterally close in front of the wings of the ovary, and hence between them and the vas deferens and uterine tube. When empty, they have a minimum diameter of only 3μ. The vitelline follicles, as shown in figure 86, occupy almost the whole of the cortical parenchyma between the longitudinal muscles and the nuclei of the subcuticular cells. They are ellipsoidal in shape, their longest diameters being directed at right angles to the surface of the strobilia. They are longest near the median line and smallest at the edges of the strobila. In general they may be said to be arranged in two

lateral fields continuous from proglottis to proglottis, but the latter are united dorsally and ventrally between the sets of genitalia by the largest which are somewhat more numerous and irregularly arranged ventrally. The average maximum depth, width and length, of the individual follicles are 70, 50, and 45μ, respectively, while the diameter of the smallest lateral follicles, more nearly spherical in shape, is about 25μ. Their number as calculated from sections averages from 800 to 1000 for each set of reproductive organs. The shell-gland is situated dorsally and to one side of the median line, the beginning of the uterine tube occupying the other side of the generative space. The latter is here not so much a space enclosed by the ovaries as the region of union of the proximal portions of the generative ducts. That part of the oviduct with which the cells of the gland are connected is only about 60μ in length. Beyond the ootype the oviduct gradually enlarges as it passes to the other side to become the uterine tube. Farther ventrally the comparatively large coils of the uterine duct pass back to the same side again and occupy a space lateral to the cirrus-sac, as mentioned above in connection with the vas deferens. Just beyond the shell-gland, where the syncitial nature of its epithelium can be made out, the oviduct has a diameter of 13μ. The uterus-sac is relatively large in this species, spherical in shape and occupies one-third of the diameter of the proglottis anteroposteriorly as well as laterally. This applies to proglottides in moderate state of contraction, for in much relaxed ones it is somewhat ellipsoidal in shape with its long axis in the median line. The youngest uterus-sac which was seen to contain eggs in the largest and most relaxed strobila at hand was spherical and had a diameter of 0.15mm., while the largest of the same chain, also spherical, was 0.50mm. in diameter. But even when they appear circular in outline from a superficial view, they are not in reality spherical since they lead off funnel-wise ventrally to the uterus-opening. The superficial aspects of the latter have been already dealt with above, so that it will be necessary to state here only that it has quite the same structure as that of *B. scorpii*, and that the actual aperture when formed is irregularly circular in outline with a transverse diameter of 60 to 85μ. The wall of the uterus-sac just within the opening is in many cases broken up into numerous processes, evidently cuticular in their nature, which protrude thru the aperture.

The egg is ellipsoidal in shape during life, and from 62 to 66μ long by 42 to 45μ wide. None were found to contain oncospheres, but only masses of cells such as shown in figures 106 and 107, the smaller of which obviously represents an earlier stage in the division of the latter. While most of these cells are yolk-cells, the large one shown at one end of figure 106 is the undivided egg. The granules of figure 107 are those resulting from the breaking down of the yolk-cells. Eggs sectioned in the uterus-sac showed similar stages in development and confirmed these statements. These measurements and drawings were made on August 2, 1912, so that it is probable that the development of the oncosphere is completed in autumn.

Concerning the life-history of this species it may be said that many of the earliest formed segments are lost long before they become sexually mature,

since most of the youngest strobilas were found lacking the end proglottis. Constrictions at about the middle were present in many of them, as if the length of segments behind that region might be thrown off as a whole. Since, however, this is not a constant feature, it is considered to be due rather to the fixation of a wave of contraction passing over the strobila, such as may be seen in living individuals as well as in plerocercoids of other genera of cestodes, e.g., *Scolex polymorphus*.

From the foregoing description it is to be seen that this species of cestode is new. The specific name, here chosen, has reference to the peculiar shape of the scolex as seen from the side: *cuspis*, an arrow-head.

The material studied consisted of Nos. N.B. 6a, N.B. 6d, N.B. 6g, No. 47, No. 50a, No. 54c and P.B. 2 from *Stizostedion vitreum*, N.B. 38a, 08107, 08108, 08109 and 08110 from *Stizostedion canadense*, and Ha 34a and Ha 35a from *Hiodon tergisus*, in the collection of the University of Illinois; Nos. 398, 423 and 481 from *S. vitreum* in the collection of Dr. H. J. Van Cleave; Nos. 7b from *Percina caprodes* and 421 from a "Pickerel" in the collection of Dr. G. R. LaRue; twelve toto preparations from *Perca flavescens* in Dr. A. S. Pearse's collection; and Nos. 41, 170, 172, 173, 174, 193 and 194 from *S. vitreum* in the writer's collection. The material from *Perca flavescens* was larval, while that from *Percina caprodes* was mature but of a small size.

BOTHRIOCEPHALUS MANUBRIFORMIS (Linton 1889)

[Figs. 26, 27, 62, 73, 87, 88, 97]

1889	*Dibothrium manubriforme*	Linton	1889 : 456
1890	*Dibothrium manubriforme*	Linton	1890 : 728
1898	*Dibothrium laciniatum*	Linton	1898 : 425
1898	*Dibothrium manubriforme*	Linton	1898 : 429
1899	*Bothriocephalus laciniatus*	Lühe	1899 : 43
1900	*Bothriocephalus manubriformis*	Ariola	1900 : 410
1901	*Dibrothrium laciniatum*	Linton	1901a : 437
1901	*Bothriocephalus kistiophorus*	Shipley	1901 : 209
1902	*Bothriocephalus manubriformis*	Porona	1902 : 7

Specific diagnosis: With the characters of the genus. Large cestodes up to 220mm. in length by 5mm. in maximum breadth. Scolex large, elongate, with prominent terminal disc deeply notched laterally as well as surficially, constricted posteriorly; length 2 to 3.5mm., depth at middle, 1.0, breadth of disc, 1.0. Bothria long and very narrow posteriorly where the walls are quite thick. First segments cuneate with salient posterior borders which are distinctly emarginate; middle, broadly cuneate, less emarginate; posterior or mature, many times broader than long and closely crowded, 5 by 0.2mm.; gravid proglottides, 2 by 0.4mm. Posterior half to two-thirds of the strobila provided with a median line (the combined uterus-sacs).

Cuticula 4.5μ thick. Calcareous bodies large, 18 to 26 by 11 to 15μ. Longitudinal muscles well developed, in bundles. Anteriorly four chief excretory vessels.

Genital cloaca median or slightly displaced towards either side, deep and narrow, separated from hermophroditic duct by a narrow velum, half way between anterior and posterior borders of the proglottis. Vagina opens immediately behind cirrus or very slightly to one side.

Testes ellipsoidal in shape, 64 to 75μ wide, 45 to 60 long, 64 to 80 deep; 60 to 70 in number, dorsal in the medulla. Vas deferens closely applied to inner end of cirrus pouch, 85μ long, 175 wide and 400 thick, somewhat crescentic in the dorsoventral-transverse plane, opposite the uterus-sac. Cirrus-sac long and cylindrical, 0.50 by 0.14mm., inner half deflected towards the vas deferens, walls very thick, composed mostly of circular muscles. Cirrus short, usually not extending outside of the proglottis, 30 to 35μ in diameter.

Vagina with bulbous sphincter near its opening, 50μ long by 70 in diameter. Ovary irregularly branched but compressed anteroposteriorly, 0.45mm. wide; isthmus only ventral. Oocapt 30μ in diameter. Vitelline follicles extremely numerous, 35μ long, 60 wide and 85 thick. Vitelline reservoir large, 60μ in diameter. Uterine duct voluminous on both sides of the median line, crowding all other organs. Uterus-sacs alternate irregularly from side to side, each 0.45mm. in diameter, encroach greatly on neighboring segments, with thick musculo-glandular funnel-shaped ventral portion. Apertures form two lines on the ventral surface 1mm. apart.

Eggs 58 by 34μ, dark brown, showing thru walls ofuterus-sacs.

Habitat: Intestine of the host.

HOST	LOCALITY	COLLECTOR	AUTHORITY	
Tetrapterus albidus (type host)	Woods Hole, Mass.	Linton	Linton	1889 : 458
Histiophorus gladius	Newport, R. I.	Linton	Linton	1890 : 731
Tarpon atlanticus	U. S. N. M.	.....	Linton	1898 : 435
Istiophorus nigricans (=*H. gladius*)	Woods Hole, Mass.	Linton	Linton	1901 : 448
Tetrapterus imperator (=*T. albidus*)	Woods Hole, Mass.	Linton	Linton	1901 : 447
Histiophorus sp.	Indian and Pacific oceans	A. Willey	Shipley	1901 : 209
Tetrapterus belone	Portoferrajo, Id. Elba	Damiani	Parona	1902 : 7

Type specimen: No. 4711, Coll. U. S. National Museum.
Co-type: No. 16.461, Collection of the University of Illinois.
Type locality: "Penekese?"

Although this species was first described more or less in detail by Linton (1889:456) and further notes were added by the same worker in the following year (1890:728), the writer feels that there is still much to be learned about it in spite of the fact that Ariola (1900:410) was able to indicate the genus to which it belongs and to correct some errors concerning the arrangement of the

bothria in his rather brief description, which is inadequate for diagnostic purposes. Consequently an attempt is here made to better define the species so far as can be done with the poorly preserved alcoholic material referred to immediately above.

In general appearance the worm arrests attention on account of the very closely arranged posterior genital segments, which give that part of the strobila a transversely plicate aspect. On closer view the anterior segments with their "salient" posterior borders and the characteristic scolex are seen (Figs. 26, 62). The latter was described by Linton as follows:

"Head cuneate, tetrangular, truncate in front, tapering posteriorly into a cylindrical neck-like part near posterior, then expanding so that the posterior end of the head resembles one of the anterior segments of the body. The general appearance of the head when viewed laterally [surficially] is therefore somewhat like a ball-bat, the constricted part representing the handle. Two longitudinal fossae [bothria], laterally placed, extend from the anterior part of the head to the constricted part. Each of the marginal lobes thus formed is indented at the anterior extremity by a short but deep [only in much contracted material] secondary fossa, which together with the two lateral fossae, give the head when viewed in front a four-lobed appearance. The edges of the lobes bordering the lateral fossae [the walls of the bothria] are thin-lipped and flexible; anteriorly there is a transverse elevation forming both a lateral and a marginal rim and making an obtuse angle between the front and the side of the head." This is the pyramidal or somewhat conical terminal disc, so characteristic of the scolex. (Figs. 26, 27). The walls of the bothria are "thin-lipped and flexible" only when protruded considerably; in moderate states of contraction, that is, nearest to what the writer considered to be the probable state of rest, they are comparatively thick and especially so in the posterior half of the scolex where in consequence the bothrium is reduced to a narrow vertical slit. "The marginal lobes, when at rest, have a rounded outline, fullest in the middle, tapering posteriorly, appressed slightly anteriorly, and raised into two small eminences on each side of the secondary fossae. The head in a marginal view is somewhat flask-shaped. Seen from the front the head is squarish, with the angles rounded and the sides deeply cleft, the clefts rounded, the lateral clefts deeper than the marginal."

As regards the segments Linton in continuation stated that: "Immediately back of the head the segments are very narrow, and for a greater or less distance, depending on the state of contraction, maintain about the same width as the base of the head. In some individuals the small anterior segments continue much farther back from the head than in the one figured. The segments are alternately short and long. This characteristic is quite plainly marked in the segments which immediately follow the head, is still noticeable on the median segments and also on the posterior ones, but is not so plainly marked on the latter as on the two former." This is due to the manner of subdivision of the segments which is carried out in the same way as in *B. scorpii* and *B. cuspidatus*. It can be followed with certainty, however, only in the "anterior"

and middle portions of the strobila and not posteriorly where the segments are very short and crowded close together longitudinally, even tho the latter may not show the rudiments of the reproductive organs. Figure 62 is an outline of a primary segment, the fifth from the scolex in this case, to show this method of subdivision. Dominance of the anterior over the posterior half of the segment as regards rate of division is well shown; and this is seen to be applicable also to the subsegments even to those of the fourth order. "In one specimen examined," to continue to quote from Linton, "the first six segments did not show this alternation in size. In the next fourteen segments, however, the alternation was quite evident." This indicates that he noted the division of the segments into subsegments but did not ascertain the exact manner in which it is carried out. "The small anterior segments are terete, subtriangular in outline, narrow in front, wide behind, the length nearly equal to the greatest breadth." It is rather difficult to say to what segments or subsegments the latter part of this statement refers, since it describes not only what is here considered to be the first primary segment, i.e., the largest segment immediately behind the scolex as shown in the figure 26, but also many of the major subsegments of the following primary segments —not all, however, since as indicated in figure 62, the dominance in division mentioned above renders subsegments of the same developmental value different in size. Furthermore, as regards these anterior segments it must be emphasized that their prominent or salient posterior borders are distinctly emarginate, which condition, very obvious in the segments immediately behind the scolex, can be followed back to the region where the segments get very broad and short. Concerning this notching of the posterior border, Linton (1889:458) said: "The segments of the first series are sometimes notched or crenulated on the posterolateral margin, with a single median indentation; in others the edge is but slightly wavy; in others it is nearly entire." In the material at hand, however, this emargination was found as just described in all of the specimens, altho in much contracted strobilae it is at first sight apparently absent. "The succeeding segments are much broader than long. At the widest part the ratio of the breadth to the length is as much as fourteen to one. As the segments increase in width they become much crowded together and thickened. . . . The crowding together of the median segments is not due to contraction, but seems to be a permanent characteristic of the species." Concerning the posterior segments Linton noted further (1890:729) that in the dead specimen taken from *Histiophorus gladius*, actually No. 16.461 referred to above, "The margins of the strobila are apparently entire. The segments are very short, with their posterior edges slightly wavy on the median segments, thus suggesting those of *D. plicatum*. The posterior edges of the median segments are crowded together like the edges of the leaves of a book about 0.2mm. apart. Near the posterior end they are not so closely crowded, being about 0.4mm. apart." (Fig. 73). Confirmatory frontal sections showed that this "entire" nature of the edge of the strobila is in reality due to partial decomposition; yet at the same time the surficial portions of the posterior borders of

the segments did not seem to be much affected. In addition it should be noted that besides being "not so closely crowded" the segments at the extreme posterior end of this strobila are relatively much narrower, as a matter of fact, only two-fifths as wide as the widest part of the strobila. This seems to be quite comparable to the elongation of the posterior end of Schistocephalus when it reaches the final host and matures.

Another important characteristic, which should be mentioned here in dealing with the external features, is that "In alcoholic specimens a dark median line will be noticed extending from the posterior end to the middle or anterior third of the strobila. This is due to the centrally situated ovaries [uterus-sacs] which are crowded with eggs;" while "a median furrow on one of the lateral [surficial] faces of the body begins toward the anterior and becomes punctate towards the posterior region, where the minute lateral genital apertures become visible in a zig-zag row."

The following table gives comparative measurements of several strobilas, the first columns being the data given by Linton:

Specimen	1	2	3	4711, U.S.N.M.		16.461
				Data by Linton	Data by the writer	
Length of strobila	133mm.	140mm.	20mm.	115mm.	.....	220mm.
Length of scolex	3.50	3.00	2.10	2;2.5;1.5	2.0	.....
Breadth of terminal disc	1.00	0.90	0.80	1;1;1.2	0.94	.....
Breadth just behind terminal disc	.....	0.80	0.60	.....	.....	.....
Breadth at middle of scolex	.....	.....	.....	.....	0.64	.....
Breadth at constriction	.....	0.21	0.31	.....	0.44	.....
Breadth posteriorly	.....	.....	.....	.....	0.81	.....
Depth of terminal disc	.....	.....	.....	.....	0.89	.....
Depth at middle	.....	0.90	.....	.....	1.05	.....
Depth at constriction	.....	.....	.....	.....	0.58	.....
Depth posteriorly	.....	.....	.....	.....	0.63	.....
Length of first segment	.....	.....	.....	.....	0.39	.....
Breadth of same anteriorly	.....	0.42	0.28	.....	0.54	.....
Breadth of same posteriorly	.....	0.80	0.50	.....	0.89	.....
Maximum breadth of strobila	.....	.....	0.90	3.5	.....	5.0
Length of widest segments	.....	.....	0.12	.....	.....	.....
Breadth of posterior end of strobila	.....	.....	.....	.....	.....	2.0
Maximum thickness of same	.....	.....	.....	.....	.....	1.5

Concerning the cuticula little can be said, since the material studied was very poorly preserved. Only in sections of a very young strobila was it seen with any degree of certainty. There it was found to be about 4.5μ in thickness, and divided by differences in degree of staining into a dark outer one-

third composed of very closely set "cirri" and an inner two-thirds, which took the stain with great avidity, leaving only a thin outer lighter part which by its contrast in color with the cirrous stratum served to set the latter off distinctly from the much thicker inner and more homogeneous part. The cuticula was not found to be in any way specially modified on the scolex, altho such might be found to be the case in well-preserved material. It was naturally retained in its entirety only within the bothria.

Only in the smallest strobilae could the subcuticula be made out satisfactorily. It is from 25 to 40μ in thickness, and composed of somewhat conical cells, the inner ends of which are quite cylindrical while the outer are much branched, divergent and interlacing. Hence the cylindrical portions, proximal to the nuclei and usually somewhat smaller in diameter than the latter, are seen to stand out distinctly and quite separately from the much less dense underlying parenchyma. The outer dendritic portions cannot be allotted with certainty to their proper cell bodies on account of this complicated mesh-work which they form just beneath the cuticula, but they can be followed to the cuticula, their attachment to which is readily seen.

Chalk-bodies in the poorly preserved parenchyma are usually elliptical in outline, with maximum lengths and widths of 18 to 26 and 11 to 15μ, respectively. They are fairly numerous and scattered thruout all parts of the strobila, being most plentiful in the cortex of ripe proglottides. In the scolex a very few small ones are to be found only in the enlarged posterior portion of the organ, where they are confined to the medulla, no doubt on account of the great development of the musculature. They are also more numerous perhaps in the medullary portion of the parenchyma of the anterior segments than in the cortical region. In general it would seem that they are developed in that portion of the parenchyma which is little occupied by other tissues or organs, chiefly muscles or genitalia.

The musculature of this species is very well developed and powerful. It was described by Linton (1890:729); but since his description is somewhat difficult to follow, the main features of its arrangement will here be given even at the expense of reporting much that has already been reported.

The frontal series is well developed and consists of two layers on each surface of the strobila, an outer, just outside of the thick layer of main longitudinal muscles, and an inner, just within this or bounding the very thin medullary parenchyma outwardly, as shown in figure 87. In the anterior segments a third series of frontal fibres appears as the posterior flaring border of the segment is approached. It forms a ring around the whole strobila, i.e., connecting with its fellow of the opposite surface laterally, unlike the other two layers, just within the subcuticula or a little more than half way from the outer edge of the layer of main longitudinal fibres to the cuticula. This series as evidently pointed out by Linton, divides just ahead of the bay behind the posterior border of the segment, part of it going to the outer, posterior border and the rest remaining within. While the latter as just indicated does not go far posteriorly, the former passes to the hinder edge of the salient border. In

mature proglottides the layer of frontal fibres just external to the main longitudinal group is greatly thickened close to the posterior border of the segment. There it forms a transverse ropelike strand, no doubt owing in part at least to the numerous vitelline follicles situated in the cortex between these levels. And this statement applies in like manner, but especially more towards the median line of the strobila, to the innermost series of frontal muscles. These, however, are further interfered with chiefly by the uteri and cirrus-sacs.

The sagittal or dorsoventral fibres are quite prominent on account of the fact that they are arranged in bundles which in the anterior segments find their way from the medulla out into the cortex between the fasicles of the main longitudinal series. They are less numerous laterally than medially. In mature segments, on the other hand, they are crowded and somewhat obliterated medially by the large genital organs, and are consequently more numerous laterally, that is, beyond the edges of the uterus-sacs. Longitudinal sections show that large numbers of them pass to the tip of the salient posterior borders of the segments and hence serve to retract the latter.

The longitudinal muscles are present in two groups, an inner, or main, and an outer series. The former appears as a very conspicuous layer of large fibres arranged in fasicles or bundles on each surface of the strobila and occupying one-half or more of the dorsoventral diameter of the cortical parenchyma. The latter are on the average much smaller, less numerous, more dispersed, and situated in the portion of the cortex between the outer frontal fibres and the cuticula. In the anterior segments the layer of inner fibres is about 70μ in thickness in the median line, and thins out gradually laterally where it joins its fellow of the opposite surface by a few fibres which lie in the plane of the flat, ribbon-like medulla (Fig. 87). Linton does not seem to have noticed this lateral union of the two layers, since he said that "It [the longitudinal muscle layer] is, moreover, interrupted at the margins where it is penetrated by the margins of the inner core [the medulla]." Farther back where the segments become very broad and short it averages about 85μ in thickness, while in mature proglottides the thickness amounts to 145μ. At the same time the fasicles, in the anterior segments quite rectangular in outline, the longer diameter being dorsoventral in direction, become more elliptical in transection. In the latter case the individual fibres are circular to elliptical in transverse section and have a maximum diameter of 15μ. In describing this group of longitudinal muscles in "transverse sections made thru that part of the body which is immediately in front of the segments that contain ripe ova," Linton stated that they ". . . are very large, altho not at this point in distinct fasciculi." This was not found to be the case in the sections studied by the writer, since fasciculi were seen all along the strobila even in the base of the scolex, altho it is true that anteriorly they are separated by only a small amount of parenchyma besides the bundles of sagittal fibres passing between them. As regards the other series of longitudinal fibres Linton rightly observed that "the longitudinal fibres of the inner part of the granular layer [here described as the outer portion of the cortex] do not differ essentially from those of the longi-

tudinal muscle layer proper, except that they are more scattered. . . ." Centrally the individual fibres of this group are of the same diameter as the smallest of the main group, while peripherally they dwindle in size as they approach the cuticula to such an extent that there they are indistinguishable from the longitudinal cuticular fibres. Longitudinal sections show that they bear the same relations to the salient posterior borders of the segments as are described here for *Clestobothrium crassiceps* and other species and emphasized by Lühe (1897a). Anteriorly a number of them pass off into the posterior border in the typical manner; but, as might be expected, they are comparatively scarce in the posterior reaches of the strobila. Again, Linton stated that "the longitudinal muscular fibres in general do not lie parallel with each other." This was found to be more strictly applicable to those within the fasicles, since only a comparatively few fibres pass from fasicle to fasicle longitudinally. But, as in other species, they are continuous from segment to segment as are indeed all of the groups of muscles, so that as far as their general arrangement is concerned, Linton's (1890:731) statements are thoroughly justified:

"Longitudinal sections were carried thru several contiguous segments. In these there were no septa to indicate a division of the body into true segments. The only indication of a segmented condition is the superficial character of the projecting posterior edges. The longitudinal muscles are continuous and the ovaries [uterus-sacs] are crowded together so as to form an almost unbroken zig-zag line. So far as any internal characters go, the body is practically continuous."

The musculature of the scolex is especially well developed, the sagittal and radial fibres being very numerous. An unusual augmentation in the number of the former appears towards the outside of the walls of the bothria, extending from the dorsal to the ventral surface. Their exact course is obscured somewhat laterally in the median frontal plane by the interdigitation of the radial fibres which takes place there, that is, opposite the lateral grooves. As the posterior borders of the scolex are approached they diminish in number and size and eventually disappear. Coming into the base of the scolex as an elliptical ring in cross-section with its thickness almost as much laterally as dorsoventrally, the layer of main longitudinal muscles soon sends out dorsoventral horns into the walls of the bothria on each side and becomes arranged in general much as in *Clestobothrium crassiceps*—doubtless an adaptation to the almost closed nature of the bothria. The outer longitudinal fibres are arranged on each side of the scolex as a continuous lateral band between the lateral sagittal fibres just mentioned and the cuticula, and extending from the dorsal to the ventral surface. Each bothrium has a much smaller and thinner band on each side next to the cuticula lining its cavity. The terminal disc is almost completely filled up with very powerful longitudinal arcuate fibres for the protrusion of its edges.

In the anterior segments the two chief nerve strands are situated in the medullary parenchyma between the lateral and median quarters of the transverse diameter of the strobila. From 18 to 30μ in diameter, they fill up the

whole of the medulla dorsoventrally at these points. In mature proglottides they have the same relative positions in the frontal plane, but are located in the ventral one-half of the medulla, their transverse diameter being as much as 50μ. In the scolex each expands opposite the edges of the terminal disc to form a ganglion, which sends out a large branch to each of the two quadrants of the disc on the same side, and connects with its fellow by a slightly narrower commissure.

Four main longitudinal excretory vessels maintain a constant course thruout the anterior segments. These are arranged in two pairs, a more median and a lateral, not in the same plane in the medulla. The members of the latter are the larger and are situated at the sides of the median one-quarter of the transverse diameter of the segment. All of these vessels are connected at various levels by large branches to form an extensive plexus thruout the medulla. In the posterior crowded segments, however, the main vessels become lost in the plexus, altho here and there they seem to occupy their original positions thru a few sections. Only two large vessels, probably the lateral pair, giving off many branches of the same calibre, can be followed with certainty into the scolex. About half way to the summit of the terminal disc they break up into a plexus which ramifies thruout the walls of the bothria. The posterior end of the smallest strobila at hand showed the same sort of communication of a terminal plexus with the exterior thru large side branches and foramina secundaria as in *B. scorpii*.

Linton (1889:457) described the reproductive organs in general in the following words: "In alcoholic specimens a dark median line will be noticed extending from the posterior end to the middle or anterior third of the strobila. This is due to the central situated ovaries [uterus-sacs], which are crowded with eggs. The genital apertures are lateral and may be traced in an irregular zig-zag line on one side from about the anterior third of the body. In the mature segments they are rendered obscure, if not wholly obliterated, by the mass of eggs with which the center of the segment is filled," and later (1890: 729, 730) besides giving the external features, quoted above, stated that "The reproductive apertures are near the median line on one of the lateral sides. They are very close together and rather small. Each aperture represents a pair of sexual organs, cirrus and vagina. Upon making a few longitudinal sections on the lateral [dorsal] face which bears the reproductive apertures, the small vaginal opening comes into view. It opens into the common aperture from behind and near the surface. The large aperture continues into the cirrus-bulb. . . . " Linton correctly stated that the common genital openings are arranged "in a zig-zag row" in the median line, as shown in figure 73; but much of this irregular lateral displacement in the mature proglottides would seem to be due to lateral pressure exerted by other organs, probably the gorged uterus-sacs or at least the uterine ducts, since in immature segments where the cirrus-sacs are already well developed, they are almost exactly in the median line. In sagittal sections the genital cloaca is seen to open to the exterior at about the middle of the length of the very short mature proglottis

and to be in many cases just covered by the posterior border of the segment immediately ahead. It is in the form of a narrow tube, often somewhat enlarged ventrally, with a length of from 85 to 115μ and extending at right angles to the general surface of the strobila. A secondary genital cloaca or ductus hermaphroditicus is present at the bottom of this tube and is separated from the latter by a valve-like muscular extension of its walls (Fig. 88). Behind this the cirrus is often found partially extended and directed backward towards the opening of the vagina or actually in contact with the vaginal sphincter. No sphincter muscle surrounding the genital cloaca at any level was found, altho a number of frontal fibres of the body muscles, curving around the structure both ahead and behind have the general appearance of such a structure. Very early traces of the reproductive rudiments were found in sections of segments 75mm. from the tip of the scolex of one of the largest strobilas studied.

The testes, continuous from proglottis to proglottis, are spherical to ellipsoidal in shape, with their longest axes usually transverse in the latter case. The measurements from sections are as follows: width, 64 to 75μ; length, 45 to 60; depth, 64 to 80. On account of their being closely and irregularly crowded in the very short segments no attempt was made to count them directly; but the average number in the transverse sections (22 to 23) multiplied by the average for each proglottis from sagittal sections of a long series of segments (3 to 4) gave about 67. The correct number is probably between 60 and 70. They are arranged in a layer in the dorsal half of the medulla, where they show some tendency towards stratification. A few, however, were found outside of the medulla, that is beyond the inner frontal muscles and between fasciculi of the main longitudinal musculature.

The vas deferens forms a compact mass of coils, closely applied dorsolaterally to the proximal deflected end of the cirrus-pouch, and alternating irregularly from side to side constantly opposing the uterus-sac. In ripe proglottides it is quite compressed anteroposteriorly by the uterine tube, and also, as a consequence, often extends thruout almost the whole of the medulla dorsoventrally, in which case it is crescentic in outline in transverse sections with the concave side directed towards the median line so as to somewhat surround the cirrus-sac. The average measurements of the mass of coils are: length, 0.085mm; width, 0.175; depth, 0.400. While it was found impossible to measure satisfactorily the size of the duct, gorged with sperms in the mass, it was seen to enter the base of the very muscular cirrus-sac with a diameter of 7.5μ. Within the latter it expands to 15μ and proceeds with this caliber in the form of a compact lot of close and somewhat spiral coils for about one quarter of the length of the pouch. In the second quarter, i.e., from the ventral end of the sac, it pursues a straight course and evidently functions as a quite efficient sperm receptacle since it is here usually from twice to three times as large as before. In the dorsal half of the pouch it again dimishes to from 5 to 7μ and continues still in a straight course to the opening as the cirrus proper. Thruout its whole course its wall is very thin, including only a very

few circular and longitudinal muscle fibres. Distally the cuticular lining is reduced to a minimum. Thus the cirrus when protruded, usually for a short distance only, is a comparatively weak structure with thin walls, but a diameter at the base of from 30 to 35μ. It is also quite short since in no place in the sections made was it found extended more than half way to the external opening of the genital cloaca, but more often, as noted above, turned around in the ductus hermaphroditicus towards the vaginal opening. Thus it is evidently adapted to the function of simply conveying the spermatozoa to the latter orifice in the act of self-impregnation rather than of acting as an intromittent organ in cross-fertilization. The diameter of the retracted cirrus was given by Linton (1890:730) as 0.008mm.

The cirrus-sac is comparatively long and cylindrical and extends from the inner boundary of the genital cloaca to the median frontal plane of the proglottis. While its dorsal half is situated more at right angles to the surface, its ventral half bends over in the transverse plane to the right or left to become related to the coiled vas deferens in the manner described above. This deflection of its proximal end thus alternates irregularly with the latter, and is always away from the uterus-sac. The maximum length and diameter in the latter case in the dorsal half of the organ are 0.500 and 0.145mm., respectively. As shown in figure 88, and as noted by Linton, the walls are very thick, leaving only a comparatively narrow cavity to accommodate the cirrus; they are composed of a very powerful inner layer of circular muscles surrounded by a thin layer of longitudinal fibres which do not have any points of attachment to the body-wall, so far as could be determined. The space surrounding the ejaculatory duct and cirrus proper accommodates the fine and quite long retractor fibres and a small amount of parenchymatous tissue. The retractors are not, however, as large or numerous as in the previous species of the genus in which the cirrus is better developed.

The vagina, which opens close behind the cirrus and usually somewhat towards the same side to which the latter is deflected, begins with a bulb-like sphincter, quite like that described and figured by Linton (1898:436) for his *Dibothrium laciniatum*, 60μ in length by about 90 in maximum diameter. The walls of this structure, 40μ in thickness, are composed of two layers of muscle fibres of equal thickness: an outer of loose circular, and an inner of somewhat radially arranged fibres. The whole organ would thus appear to be adapted to the pumping of the sperms into the vagina. The latter proceeds ventrally with a diameter of about 25μ, after enlarging considerably immediately behind the bulb. It is surrounded by circular fibres only. At the level of the ventral end of the cirrus-sac it joins the oviduct.

The ovary, which has an average width of 0.45mm., is irregularly branched in mature proglottides, much compressed anteroposteriorly by the numerous coils of the uterine tube, and often displaced from the median line by the latter and the spacious uterus-sac. Furthermore, while the isthmus, itself irregular in shape and hence somewhat difficult to distinguish from the rest of the organ, "lies next the inner side of the lateral [ventral] muscular wall," the wings

curve upward on each side, sometimes reaching almost to the dorsal boundary of the medulla. The oocapt is almost spherical in shape with an average diameter of 30μ, and is situated in the median line. The oviduct immediately beyond the narrow outlet of the oocapt is 25μ in diameter. At the point of union of the vagina with the oviduct there seems to be a vestibule, similar to that of *B. scorpii*, but this was not made out to the writer's satisfaction. Two vitelline ducts, each about 15μ in diameter, unite at about the level of the oocapt and continue dorsally with the same diameter as the common vitelline duct. This turns downward again and quickly enlarges to form the vitelline reservoir, which was found to have a maximum diameter, when filled with yolk cells of about 60μ. The vitelline follicles are extremely numerous and very closely arranged in the cortical parenchyma in two lateral fields, a median strip being left free of them on each surface of the strobila. They are ellipsoidal in shape, with average maximum lengths, widths and depths of 35, 60 and 85μ, respectively. In the material studied they showed considerable tendency towards stratification and on account of this fact, their very varying size and the poor condition of their walls, no satisfaction was experienced in attempting to determine the approximate number for each segment; but it must be well over one thousand from a comparison of the sections with those of *B. cuspidatus*.

The uterine duct begins approximately in the median line, quickly expands between the cirrus pouch and the ovary, first in the direction of the coiled vas deferens and as far laterally as the edge of the ovary, and then crosses the median line to the opposite side where the mass of coils, occupying the whole dorsoventral diameter of the medulla, further enlarges gradually in all directions and joins the comparatively large uterus-sac. In toto preparations the duct and sac are seen to form a continuous club-shaped mass gorged with eggs and with the larger end, the sac, alternating irregularly from side to side. This irregular alternation of the uterus-sacs was evidently not noticed by Linton since he spoke of only "a dark brown median stripe made by the ripe ova in the crowded ovaries [uteri] "; but Ariola (1900:410) said of them: "Le masse ovariche spesso sono irregolarmente collocate da una parte e dall' altra della linea mediana." Only in sections can one distinguish the sac from the duct, since the two are so closely applied to each other. In dorsoventral view the uterus-sac, itself, is somewhat circular in outline, when not pressed against one of its fellows ahead or behind, and has a maximum diameter of 0.45mm. Ventrally, however, it is funnel-shaped. As shown in figure 73, it may become so enlarged as to invade the adjoining proglottides to a considerable extent. The aperture is located in the middle of the sac and consequently forms with its fellows two lines of irregularly alternating pores on the ventral surface of the strobila, about 1.0mm. apart. It is only about 20μ in diameter, and is situated towards the anterior border of the proglottis, often well under the overlapping posterior border of the segment ahead. The lowermost or funnel-shaped portion of the sac, little more than that which passes through the stratum of longitudinal muscles, is surrounded by a thick layer of material, as shown in figure 97, the nature of which was not determined satisfactorily. It appears

to be glandular in nature, altho muscle fibres traverse the mass in several directions, the inner of them being longitudinal and the outer circularly oblique. Altho this structure may have a glandular function in connection with the passage of the eggs to the exterior, it obviously acts as a powerful sphincter controlling the same and permitting perhaps of the laying of only a few at a time. Distal to the outer end of the funnel, where it loses these fibres, the sac continues through the cortical parenchyma as a narrow tube to the pore.

The eggs of this species were said by Linton (1889 and 1890) to be of two kinds: ". . . one yellowish in mounted specimens with a strong shell, in some cases white and opaque; another sort transparent, with a very thin shell." These differences were seen in the material studied, but they were considered to be merely due to differences of age, the thinner-shelled ones being the younger. While the same author gave the length and breadth as 45 to 54μ and 27 to 30μ, respectively, the writer found their maximum dimensions to be in sections 58 by 34μ.

The material studied consisted of two lots: No. 4711, in the collection of the United States National Museum, from the rectum of *Tetrapterus* sp. from Penekese, determined by Linton; and No. 16.461 in the collection of the University of Illinois, from the intestine of *Histiophorus gladius*, obtained from Prof. Linton, and evidently the actual specimen described by him in 1890. The details of the anatomy, here given, were studied from confirmatory sections of the latter.

DIBOTHRIUM LACINIATUM Linton

Linton (1898:425) established this species on the basis of the material contained in lot No. 4741 of the collection of the United States Museum from *Tarpon atlanticus*, and again reported it from the same host species in 1901 (p. 437). Lühe (1899:43) in his list of the species of the genus Bothriocephalus s. str. remarked that "Von weniger gut bekannten Arten gehören anscheinend noch hierher *Bothriocephalus laciniatus* (Lint.) und *occidentalis* (Lint.);" while Ariola (1900:414) also placed it in the same genus, as he conceived the latter to be constituted.

During the study of *B. manubriformis* the writer was impressed with the great resemblance between *D. laciniatum* and it, in all but a few details, the two being, in fact, identical. The measurements for length and maximum breadth, as shown in the comparative table below, agree, while those of the scolex and anterior segments are as near as can be expected from cestode material which is found in various degrees of contraction and relaxation. All of the conditions represented in Linton's (1898) Figs. 7 to 12, Pl. XXX, were observed in the material of *B. manubriformis* studied—when such obvious errors as, "Fossettes marginal as to head, corresponding to the flat surface of the body," are taken into consideration—while the description of the external features, excepting that of the posterior segments, applied in detail. But later lot No. 4741, U.S.N.M., was obtained by Professor Ward, and the writer

learned that his suspicions were well founded; for *D. laciniatum* proved to be identical with *B. manubriformis*. The posterior segments "with breadth one and a half times the length" had different proportions from those observed in mature material of the latter species, because they were, altho gravid, of quite youngers trobilas. The material of No. 4741 is, in fact, intermediate between No. 4711 of *B. manubriformis* and the 16.461 of the same species dealt with above, not so much in size since it does not show the regions so well, as in degree of maturity. The fact that "the segments are not uniform; one segment with a salient posterior border followed by about two with less salient borders" is due to the irregular manner in which the primary segment divides into subsegments. The dimensions of the eggs correspond, while the measurements of the cirrus-bulb, vaginal sphincter and calcareous bodies are the same in the two species. Linton stated that in *D. laciniatum* "The reproductive cloacae lie along the median line of one of the flat surfaces of the body. The external openings of the uterus lie along the median line of the opposite surface." While the former was found to be the case, the latter was not, for the openings of the uteri lie irregularly on either side of the median line as in *B. manubriformis*. Furthermore, the cirrus-bulb was not found to have "its inner end deflected to the right [left, when we take into consideration the fact that the common genital cloaca of *D. laciniatum* was considered to open on the ventral instead of the dorsal surface] where it communicates with the vas deferens, which lies in numerous folds in front and to the right of the cirrus-bulb," but to alternate irregularly from side to side according as the uterus-sac and distal end of the uterine duct occupy the other side of the proglottis; while the vas deferens was as described above (p. 142). Altho the vaginal bulb was found to be a little larger in the material of *D. laciniatum*, its structure and position were also quite as in *B. manubriformis*. On the other hand no muscle fibres completely encircling both genital apertures, such as shown in Linton's Fig. 5, Pl. XXXI, were seen, but what might easily be taken for such were formed by the crossing of much curved and spread longitudinal and transverse fibres of the body wall, in such a manner that the portions intersecting at the four corners run in almost circular directions and concentrically parallel to each other so as to give the appearance of the whole forming a complete ring in each case. The genital cloaca was found to be shallower than in the material from *Histiophorus gladius*. This is evidently due to the fact that the proglottides were younger and not yet gravid as in those from the latter host. The uterus-opening was not found to be "lined with cilia" but with irregular ragged processes which are evidently only portions of the lining of the developing funnel and the external duct of the same. Finally the position and structure of the ovary, of the vitelline reservoir and of the various layers of the body exactly correspond in the two forms.

Consequently the writer feels that there can be no doubt whatever concerning the identity of *D. laciniatum* with *B. manubriformis*, which fact also seems to be recognized in the Fauna of the Woods Hole Region (Sumner, Osborn and Cole, 1913: 585) where the former is not found among the cestodes, altho

the host, *Tarpon atlanticus*, is listed. Since *B. manubriformis* was described before *D. laciniatum*, the latter must now be considered as a *species delenda*.

BOTHRIOCPHALUS HISTIOPHORUS Shipley

The writer would also like to call attention in this place to the fact that Shipley's (1901) *Bothriocephalus histiophorus* agrees in all essentials with *B. manubriformis*, which is almost to be expected since both are found in the same host genus.

The description and figure of the scolex is that of the latter species, altho the true nature of the bothria was not ascertained by Shipley on account of their almost closed condition, which was also seen in many specimens of *B. manubriformis* by the writer. Consequently it was described, erroneously, as ". . . provided with longitudinal slit-like depressions which hardly attain the dignity of suckers situated in the dorsal and ventral plane." The external features of the strobila are the same in both species, altho Shipley was describing a comparatively young specimen, as shown in his measurements of the scolex and in his figures showing the size of the uterus-sac. The description and figures of the genitalia agree in almost all details. It is quite apparent, however, that his Fig. V, diagrammatic it is true, is entirely misleading as to the proximal connections of the reproductive ducts, one of which, the ootype, he confused with the isthmus of the ovary. The ova in the latter were found by the writer to be 15μ in diameter in *B. manubriformis* as in *B. histiophorus*. His description of these central connections of the genital ducts is certainly not that of the genus Bothriocephalus; for in dealing with the isthmus of the ovary, which he called the ootype, he said that "Into this region opens the small shell-gland, and the ducts of the yolk glands. The shell-gland lies posteriorly to the ovary between the right and left halves of that organ and with the ducts of the yolk glands it opens into the ootype posteriorly." The measurements of the eggs and the description of the uterus agree with those of Linton's species, excepting that the opening of the uterus-sac ". . . does not seem to be provided with anything of the nature of a sphincter muscle. . ." Altho the material at hand did not permit of the sectioning of such young stages in the development of the uterus-sac, it would seem from the somewhat varying nature of its funnel-shaped ventral end, described above for *B. manubriformis*, that in more anterior proglottides it might be in such a condition as to be easily overlooked. The nature and arrangement of the vitelline glands, the vagina and its bulb or sphincter, the testes in number and position, and finally the cirrus-sac, all considered in connection with his Figs. I–IV, force the writer to the conclusion that, so far as can be determined in the absence of material for study, Shipley's *B. histiophorus* n. sp. is identical with *B. manubriformis* (Linton).

Concerning the probable disposal of ripe eggs in *B. histiophorus*, Shipley made a statement with which the writer can agree, since it seems to be the natural conclusion to arrive at after a study of the varying contents of the uterus-sac along the strobila, namely, "From what I have seen I think it prob-

able that eggs pass out from the tapeworm into the alimentary canal of the host and that in *B. histiophorus* the eggs pass freely out from each proglottis and do not wait until the posterior proglottides break off to make their escape from the parent."

In the following table a number of important measurements of *B. manubriformis*, *D. laciniatum* and *B. histiophorus* are given for the sake of comparison; all dimensions are given in millimeters:

	D. laciniatum	*B. histiophorus*	*B. manubriformis*
Maximum length of strobila	154	.....	220
Maximum breadth of strobila	4	.....	5
Breadth at posterior end	2	.....	2
Length of scolex	2	1.8	1.5-3.5
Breadth of terminal disc	0.8	0.4	0.8-1.2
Breadth of scolex at middle	0.4	.....	0.64
Breadth at posterior end	0.6	.....	0.81
Breadth at constriction	0.25	.....	0.21-0.44
Depth of terminal disc	0.5	.....	0.89
Depth of scolex, middle	0.55	.....	0.90-1.05
Depth at posterior end	0.35	.....	0.63
Depth at constriction	0.25	.....	0.58
Length of first segment	0.7	.....	0.39
Breadth of same anteriorly	0.3	.....	0.28-0.54
Breadth of same posteriorly	0.65	.....	0.50-0.89
Length of median segments	0.3	0.3	.....
Breadth of median segments	0.3	.....	.....
Length of posterior segments	1	0.16 ("ripe")	1.0
Breadth of same	1.5	0.5 ("ripe")	2.50
Length of cirrus-sac	0.4	.....	0.50
Max. diameter of same	0.14	.....	0.14
Length of vaginal sphincter	0.05	.....	0.05
Diameter of same	0.07	.....	0.07
Dimensions of eggs	52x35μ	45x35μ	58x34μ
Dimensions of calcareous bodies	17-24x8-14μ	.....	18-26x11-15μ
Number of testes	.....	50-70	60-70
Diameter of ova in ovarian isthmus	.....	0.15	0.15

BOTHRIOCEPHALUS OCCIDENTALIS (Linton 1898)

[Figs. 28, 89]

1898	*Dibothrium occidentale*	Linton	1898 : 437
1899	*Bothriocephalus occidentalis*	Lühe	1899 : 43
1900	*Bothriocephalus occidentalis*	Ariola	1900 : 415

Specific diagnosis: With the characters of the genus. Large cestodes with maximum length at least 310mm. and breadth 5.5. Scolex small, elongate and somewhat rectangular, constricted posteriorly, 1.3mm. long by 0.46 wide. First segments somewhat funnel-shaped; middle, densely crowded, ten to twenty times broader than long; posterior narrower and longer, 2 by 0.8mm., in groups of three or four.

Cuticula 1.5μ in thickness. Calcareous bodies 18 by 13μ. Longitudinal muscles in bundles, outer series very scarce. Four chief excretory vessels, two much more prominent than the others.

Genital cloacae form a narrow zig-zag row, each very shallow, no velum, cloaca and hermaphroditic duct united. Vagina opens directly behind the cirrus or a little to one side.

Testes divided into two fields on each side by the nerve strand, 75 to 90 in number, 25, 85, and 115μ in average maximum length, breadth and depth. Coils of vas deferens loosely arranged, the duct 25μ in diameter, alternating irregularly from side to side opposite the uterus-sac. Cirrus long and cylindrical, 0.23 by 0.06mm., walls comparatively thin, most of the circular muscles being towards the inner end.

No vaginal sphincter nor bulb. Ovary solid, unbranched, 0.5 to 0.6mm. wide, 0.04 long and 0.13 to 0.18 deep. Oocapt 25μ in diameter. Vitelline follicles very numerous, the two lateral fields on each surface narrow, leaving a broad median strip free, 25, 60 and 115μ in length, breadth and depth, respectively. Vitelline reservoir 45μ in diameter. Uterine duct voluminous on both sides of the median line, crowding all other organs. Maximum width and length of uterus-sac, 0.65 and 0.25mm., respectively; not encroaching much on neighboring proglottides; ventral portion not especially modified. Uterus-openings alternate irregularly from side to side near the median line, far forward in the proglottides.

Eggs 72 to 76 by 38 to 41μ, dark brown, showing thru the walls of the distended uterus-sacs.

Habitat: Intestine and pyloric coeca of the "rock cod," Sebastodes sp.

Type specimen: No. 4740 in the collection of the United States Museum, collected by T. H. Bean and identified by Professor Edwin Linton.

Type locality: Whatcomb, Washington.

The material contained in lot No. 4740 of the collection of the United States Museum, upon which Linton based his species, was examined by the writer and confirmatory sections were made of mature segments; but it was all in such a very poor state of preservation that only a little can be added to the meagre descriptions already published.

Lühe (1899:43) stated under his diagnosis of the genus that "Von weniger gut bekannten Arten gehören auscheinend noch hierher *Bothriocephalus laciniatus* (Lint.) und *occidentalis* (Lint.)," while Ariola (1900:415) included it in his compendium of the known species.

Since no scolex and only very poorly preserved anterior parts of the strobila were found in the above mentioned lot, Linton's description is here given verbatim:

"The bottle contained two fragments and portion of pyloric coeca of fish. The fragments measured 190 and 310mm. in length, respectively. Another fragment with scolex was found in one of the pyloric coeca; this was 115mm. in length.

Head small, elongated truncate, and somewhat capitate, constricted near posterior end with prominent posterior margin; fossettes coincide with flat surface of body and extend posteriorly nearly to constriction; segments begin immediately behind head, somewhat funnel-shaped, soon becoming densely crowded and much broader, ten to twenty or more times as broad as long, decreasing in breadth and increasing in length again toward posterior end. Posterior segments in groups of three or four, namely, divisions between segments of contiguous groups more distinctly marked than between other adjacent segments.

Dimensions of head and segments: Length of head, 1.30mm.; breadth of head, apex, 0.46; middle, 0.46; base, 0.40; breadth of first segment, 0.42; length of first segment, 0.12; greatest breadth, 5.5; length of broadest segments, 0.25; breadth of posterior end, 2; length of posterior segments, 0.8. . . .

The sides of the head which correspond with the lateral margins of the body are medianly depressed toward anterior end."

Concerning the cuticula nothing more can be said than that in the anterior segments where it did not seem to be much eroded, it was found to be only about 1.5μ in thickness. The subcuticular cells are closely crowded together. They form a syncitioid layer, in which the comparatively large nuclei (8μ in diameter) stand out prominently, beginning about 35μ from the surface and extending centrally to the vitelline glands. As pointed out by Linton, "Calcareous bodies are present in the central core [medulla] and sparsely scattered elsewhere, but nowhere abundant. . . " The largest of them were found to be 18μ long by 13 wide, thus being within the limits of measurements of those of *B. manubriformis*.

In general the musculature is quite comparable to that of *B. manubriformis*. There is a stratum of frontal fibres on each surface of the layer of longitudinal fibres, but no third or outermost group in the anterior segments, doubtless owing to the fact that the posterior borders of the latter are not nearly so prominent. Both layers are related to the uteri and cirrus-sacs in the same way. The sagittal fibres are much less numerous especially anteriorly. While the main longitudinal muscles, arranged in quite the same manner and with the same thickness, namely, 145μ, render the cross-section of mature segments similar to that of *B. manubriformis* at first sight, the fibres of the external group

of this series are very scarce, confined to the anterior segments and very difficult to distinguish from the longitudinal cuticular fibres.

The nerve strands, each about 35μ in transverse diameter anteriorly and 85μ thick by 45μ wide in mature segments, are situated between the lateral and median quarters of the transverse diameter of the strobila. Unlike conditions in the foregoing species, they occupy either the whole of the dorsoventral diameter of the medulla or are situated strictly in the median frontal plane, depending on the degree of lateral contraction.

In the anterior segments two main longitudinal excretory vessels are located in the medulla between the nerve strands; while two others, much smaller and outside of the latter, are somewhat difficult to follow. In mature proglottides, however, all four vessels are fairly easily distinguished, especially in transections.

"The cirrus and vagina open by a common aperture on the middle of one of the flat surfaces of the body. . . . The vagina is behind the cirrus; in some cases directly behind it, in others a little to one side or other of the median line." This was found to be in the main true, altho on close examination it is to be seen that the common genital openings form a zig-zag row as in the foregoing species. The uterus-openings, described as opening "externally on the middle of the dorsal surface," likewise alternate irregularly from side to side. Furthermore, while the genital cloaca is situated at the middle of the very short proglottis, the opening of the uterus-sac is in the anterior portion of the segment, often being under the posterior border of the segment ahead. The cloaca itself is very shallow in this species, the openings of the cirrus and vagina being almost at the surface. There is no definite velum separating an inner ductus hermaphroditicus from an outer cloaca as in *B. manubriformis*.

In the sections made, the testes, divided into two fields on each side by the nerve strand, were much compressed anteroposteriorly with average maximum lengths, breadths and depths of 25, 85 and 115μ, respectively. On account of this crowded condition it was not found practicable to count their number directly in frontal sections, but it was calculated to be from 75 to 90. The vas deferens, averaging about 25μ in diameter, forms a number of loose, open coils extending thruout the whole dorsoventral diameter of the medulla on the side towards which the central end of the cirrus-sac is directed, and alternating irregularly from side to side as does the uterus-sac, but being constantly located on the opposite side of the median line from the latter. As it passes into the base of the cirrus pouch it has a diameter of only 3μ. In the proximal or central one-third of the sac it takes a few turns and then continues as a straight tube, somewhat larger (15μ) and usually filled with spermatozoa, the functional cirrus which is about 8μ in diameter. The cirrus-sac is elongate oval to cylindrical in shape, the slightly larger end is ventral, and has a maximum length and a diameter of 230 and 60μ, respectively. It is thus approximately only one-half as large as that of *B. manubriformis*; nor does it extend ventrally past the lower edge of the layer of main longitudinal muscles. Its wall, as shown in figure 89, is comparatively thin, as pointed out

by Linton, especially in the dorsal half, the inner layer of circular fibres being much more numerous ventrally. Thus there is left a comparatively large space around the ejaculatory duct to accommodate the retractor muslces and a small amount of parenchyma the nuclei of which are situated peripherally much as in *B. scorpii*. A character which distinguishes this species, however, from others of the genus is the presence of a loosely arranged bundle of muscle-fibres attached to the ventral end of the cirrus-sac and passing downwards between the coils of the uterine duct, beyond which they do not seem to have any definite attachment. Since the myoblasts and nuclei of these fibres are quite prominent, especially some distance from the cirrus-sac, the whole bundle has something of the appearance of an elongated gland. The protruded cirrus has a maximum length of 85μ with a diameter of 30μ. This everted condition of the cirrus, taken in conjunction with the nature of the genital cloaca described above, and the fact that there is no vaginal sphincter, points strongly to the cross-fertilization of at least different proglottides, rather than to self-fertilization. The former would, furthermore, seem possible between contiguous segments, since in many cases two consecutive cloacae were found close together and at the bottom of an apparently temporary depression of the dorsal surface.

The vagina has no sphincter, but begins somewhat broadly, as shown in Linton's figure 5, only to narrow down quickly to about 5μ half way along its course, which is almost straight ventrally. It expands slightly before joining the oviduct but does not form more than a temporarily functional seminal receptacle. The ovary, much compressed anteroposteriorly, is from 0.5 to 0.6mm. wide by only 40μ long at the isthmus, and from 0.13 to 0.18mm. deep. Its limbs are entire but much disturbed in their course laterally by the uterine ducts of contiguous proglottides. The oocapt has an average diameter of 25μ. Beyond it the oviduct enlarges, after constricting as usual, to about 25μ again where it is joined by the vagina. At the latter point there is a vestibule as in the last species. Just beyond this the oviduct is joined by the common vitelline duct which is enlarged near the junction to form the yolk reservoir or "central vitelline mass," about 45μ in diameter. The vitelline follicles are very numerous and closely arranged in the cortex in two lateral fields, leaving a broad median strip free of them on each surface of the strobila. Their maximum lengths, breadths and depths are 25, 60 and 115μ respectively; they have thus approximately the same bulk individually as those of *B. manubriformis*. They are continuous at the edges of the strobila and occupy the central one-half of the thickness of the cortical parenchyma, excepting in the median free strips. While the rather small shell-gland occupies a somewhat limited position dorsally at the level of the ventral end of the cirrus-pouch, the uterine duct takes so many coils, all of which are filled with eggs, in the median portion of the proglottis on both sides of the midline that most of the other structures are all but obliterated—at least at first sight. Both the uterine duct and the uterus-sac are arranged pretty much as in *B.manubriformis*; but the latter is only from 0.27 to 0.37mm. wide by about 0.15 long and about

0.35 deep in proglottides where the whole median portion is gorged with eggs. In the widest segments, however, they may attain a width of 0.65mm. by a length of 0.25 but at the same time not encroach so much on the neighboring segments as in the last species; for the length of the broadest segments, as given above, is 0.25mm. The lower portion of the sac is not modified into a funnel-shaped structure, while the actual opening is only about 15μ in diameter.

The measurements of the eggs are, according to Linton, 72 to 76μ in length by 38 to 41 in breadth. Such were found in the sections made, but no opercula such as shown in his figure 11; altho many similar appearances were considered to be only regular breaks in the shell.

From the above description it is to be seen that in many respects this species is very close to *B. manubriformis*. But in others it is sufficiently different to warrant the retention of Linton's designation, the more so in view of the fact that the host was taken from the Pacific coast, the bothriocephalid fauna of which has apparently not yet been touched.

CLESTOBOTHRIUM Lühe 1899

Bothriocephalus (part.)	Rudolphi	1819
Dibothrius (part.)	Rudolphi	1819
Bothriocephalus (part.)	Leuckart	1819
Bothriocephalus (part.)	Dujardin	1845
Dibothrium (part.)	Diesing	1850
Dibothrium (part.)	Molin	1858
Dibothrium (part.)	Diesing	1863
Bothriocephalus (part.)	Carus	1885
Bothriocephalus (part.)	Ariola	1896
Clestobothrium	Lühe	1899
Bothriocephalus (part.)	Ariola	1900
Clestobothrium	Braun	1900

Scolex almost spherical, the free edges of the dorsoventrally situated bothria fused with each other in their whole extent in such a manner that only a small surficial opening near the apex leads into the interior of the spacious, hollow organ of attachment, flattened in the sagittal direction, by means of a short almost sagitally coursing canal which can be closed by a sphincter-like musculature. External segmentation complete. Vitelline follicles in the cortical parenchyma. Receptaculum seminis small. Beginning of the uterus a winding canal which leads into an extraordinarily spacious uterus-sac, distorting all other genital organs in ripe proglottides. Uterine opening about median as is the dorsal genital opening.

Type and only species: *C. crassiceps* (Rudolphi).

CLESTOBOTHRIUM CRASSICEPS (Rudolphi 1819)

[Figs. 29-31, 48, 49, 58, 74, 75, 90, 103, 108]

1819	*Bothriocephalus crassiceps*	Rudolphi	1819 : 139, 476
1819	*Bothriocephalus pilula*	Leuckart	1819 : 45
1845	*Bothriocephalus crassiceps*	Dujardin	1845 : 617
1850	*Dibothrium crassiceps*	Diesing	1850 : 587
1858	*Dibothrium crassiceps*	Molin	1858 : 134
1863	*Dibothrium crassiceps*	Diesing	1863 : 236
1885	*Bothriocephalus crassiceps*	Carus	1885 : 120
1896	*Bothriocephalus crassiceps*	Ariola	1896 : 280
1899	*Clestobothrium crassiceps*	Lühe	1899 : 44
1900	*Bothriocephalus crassiceps*	Ariola	1900 : 397
1900	*Clestobothrium crassiceps*	Braun	1900 : 1692
1901	*Dibothrium crassiceps*	Linton	1901 : 411, 451, 473
1909	*Dibothrium crassiceps*	Johnstone	1909 : 87

Specific diagnosis: With the characters of the genus. Medium sized cestodes, up to 92mm. in length, with a maximum breadth of 1.5mm. Anteriorly surface of body with closely arranged transverse furrows, posteriorly segmentation more distict, serrate. Scolex globose, 0.64 to 1.08mm. long, 0.52 to 0.90 broad, and 0.68 to 1.21 thick; divided by longitudinal marginal grooves into two dorsoventral hemispheres, the bothria. Latter large, prominent, oval, their apertures about one-third their length from the apex and connected by a saddle-shaped groove over the tip of the scolex, with prominent lips. No neck, segmentation beginning immediately behind the scolex. Young segments closely arranged, five to six times as broad as long; mature proglottides quadrate to twice as long as broad, frequently divided on one or both sides by spurious articulations usually behind the uterus-sacs.

Cuticula 2 to 5μ thick, subcuticula 20μ. Chalk-bodies absent. Musculature well developed, powerful sphincter around orifice of bothrium. Chief nerve strands ventral, 15 to 20μ in diameter. Usually four longitudinal excretory vessels.

Genital cloaca median, dorsal, three-fourths to one-half the length of the proglottis from its anterior end, usually just posterior to the spurious articulations; hermaphroditic duct within cloaca.

Testes in two lateral fields in the medulla; ellipsoidal in shape, 0.125mm. long by 0.04 in diameter, continuous from joint to joint, 40 to 50 in each proglottis. Vas deferens forms a wedge-shaped mass of coils ahead of cirrus-sac and alongside of the hinder end of the uterus-sac. Cirrus-sac elliptical to somewhat oval, 0.128 to 0.162mm. long by 0.087 to 0.116 wide and 0.098 to 0.116 deep, immediately behind the uterus-sac or lateral to its posterior end. Cirrus-sac and vas deferens together alternate irregularly from right to left opposite the hinder end of the uterus-sac.

Opening of vagina close behind that of cirrus. Receptaculum seminis present as a short diverticulum almost parallel to the oviduct at the point of union of the vagina with the latter, about 10μ in diameter. Ovary bilobed, the isthmus narrow and ventral, ova in same 18 by 10μ. Oocapt 20μ in dia-

meter. Vestibule at the point of union of the vagina with the oviduct. Vitelline duct expands into a reservoir 30μ in diameter. Vitelline follicles not in lateral fields, but continuous from joint to joint, 60 by 30 by 50μ in dimensions, about 700 in each proglottis. Uterus-sac elliptical in outline, directed anteroposteriorly in the anterior half of the proglottis, where in gravid segments it occupies almost the whole of the medullary region; 2.20 by 1.34mm. in dimensions; in quadrate segments irregularly alternating from side to side as are the uterine openings.

Eggs, 75 by 40μ.

Habitat: In the anterior portion of the intestine of the host.

HOST	LOCALITY	COLLECTOR	AUTHORITY
Gadus merluccius (Type host)	Naples	Rudolphi	Rudolphi 1819 : 139
Gadus merluccius	.....	Leuckart	Leuckart 1819 : 45
Gadus merluccius	Patavia	Molin	Molin 1858 : 134
Gadus merluccius	Trieste	Stossich	Carus 1885 : 120
Gadus euxinus	Trieste	Stossich	Stossich 1899 : 1
Merlangus carbonarius	Nizza	Wagener	Wagener 1854 : 61
Merlangus sp.	.....	Wagener	Wagener 1857 : 93
Merluccius bilinearis	Woods Hole	Linton	Linton 1901 : 473
Merluccius esculentus	.....	Parona	Ariola 1896 : 265
Merluccius esculentus	Trieste	Stossich	Stossich 1898 : 115
Merluccius merluccius	Pisa	Wagener	Wagener 1854 : 68
Merluccius vulgaris	Ireland	Drummond	Thompson 1844 : 439
Merluccius vulgaris	Patavia	Molin	Molin 1861 : 235
Merluccius vulgaris	Pisa	Wagener	Diesing 1863 : 237
Merluccius vulgaris	Padova	Molin	Diesing 1863 : 237
Merluccius vulgaris	Genova	Parona	Ariola 1896 : 265
Merluccius vulgaris	Portaferrajo, Id. Elba	Damiani	Parona 1899 : 8
Merluccius vulgaris	Pisa	Parona	Parona 1899 : 8
Merluccius vulgaris	Gaeta	Ariola	Ariola 1900 : 397
Merluccius vulgaris	Augusta, Catania	Barbagallo and Drago	Barbagallo and Drago 1903 : 412
Pomatomus saltatrix	Woods Hole	Linton	Linton 1901 : 451
"A small hake"	Calf of Man, England	Johnstone	Johnstone 1909 : 87
Merluccius bilinearis	Passamaquoddy Bay, St. Andrews, N.B.	Cooper	Cooper (the present paper)
Merluccius bilinearis	Buzzards Bay, Mass.	Cooper	"
Merluccius bilinearis	Vineyard Sound, Mass.	Cooper	"
Merluccius bilinearis	Casco Bay, Me. South Harpswell	Cooper	"

In external appearance this species is characterized by the globose nature of the scolex and the serrate margins of the strobila, the former of which was the basis of Leuckart's (1819:45) specific name and which with the latter was emphasized and included in the diagnoses given by all the authors after Rudolphi (1819). But another important character which also assists in the ready recognition of the species is the presence of spurious articulations, which, however, are evidently not those mentioned collectively by Wagener (1854:69) as "articulatio spuria."

The scolex (Figs. 29-31) is divided by two longitudinal marginal grooves into two dorsoventral hemispheres, the bothria. The latter were considered by Rudolphi (1819:130, 477) and others to be marginal in position, but many years elapsed before this error was finally and definitely corrected by Lühe (1899:35). F. S. Leuckart (1819:45) rightly described and figured the scolex as "medio marginali sulcato, foveis lateralibus. . . ." and "Die Randfläche des Kopfes ist breiter als die Seitenfläche, die mittelfurche jener ziemlich tief, und bi det an jener Seite eine erhabene, in der Mitte hellere Wölbung." It seems that Molin (1881:235) fell into the error of considering the marginal or lateral grooves, separating the bothria, to be the bothria themselves, as indicated in his diagnosis: "Caput magnum subglobosum, utrinque sulco longitudinali laterali, apertura centrali bilabiata antica, bothriis ovalibus, subter minalibus, marginalibus, longis"; and in his "Osservazione 2" he said: "Quantunque la testa sia molta grossa ed opaca, ciò non per tanto potei distinguere il solco menzionato da Diesing [1850:587] il quale pero corrisponde ai lati e non ai margini del corpo, e sembra dividere la testa in due emisferi. Ognuno di questi porta una fossetta oblunga, ovale, che si estende dall' apice a due terzi della lunghezza del corpo, e sembra di quattro quadranti suddivisi da due solchi che s'incrocciano." It is evident from his figure 2, Taf. V, that the "fossetta oblunga" is the entrance to the bothrium, but he does not seem to have observed the actual opening. Matz (1892:103) expressed the opinion that the bothria of this species are dorsoventral in position, while Ariola (1896:280) evidently on the basis of former descriptions placed the species among those of the genus Bothriocephalus Rud. with "Botridi marginali." Stossich (1898: 115) also described the scolex as " . . . subglobosa, con botridii marginali, subterminali, ovato-allungati." Ariola (1900:398) finally corrected his own view of the external structure of the scolex by saying that "Un esame anche superficiale dimostra però che la posizione degli organi di fissazione non e equale fu ritenuta, perchè ciascun d'essi corrisponde ad una faccia larga dello strobila, o como si dice, sono dorsoventrali. I pretesi botridii marginali sono dati da un solco circulare, abbastanza profondo, che corre a guisa di un meridiano attorno allo scolice globoso, passando per l'apice, e dividuendolo come in due emisferi, uno destro a l'altro sinistro," thus evidently ignoring the fact that Lühe had already (1899:25) performed the service for students of the group, as he later pointed out with justifiable emphasis (Lühe, 1901:414).

The bothria in this species are sac-like structures, formed (phylogenetically) as indicated in the generic diagnosis, by the rolling together of their edges or

"walls" and the fusion of the latter for most of their extent "in such a manner that only a small lateral [dorsoventral] opening in the region of the apex leads into the anterior of the spacious, hollow organ of attachment." The size and shape of the opening itself varies considerably in preserved material. It may be so small (Fig. 29) as to be seen only on very close examination or in sections, or comparatively large (Fig. 49), depending on the stage of contraction or enlargement of the bothria when the individual is fixed or preserved. During life it may be seen to undergo such variations in size while the whole scolex isbeing elongated and retracted during the characteristic sucking movements. Rudolphi (1819:477) correctly described the bothria as ". . . oblonga profunda et magna in vivis; in mortuis bothrii ostium parvum anticum adesse videtur." In lateral view (Fig. 30) the bothria are seen to be more sharply oval or even conical in outline, as is consequently the whole scolex, owing to the fact that the dorsoventral diameter of the lumen of each is much greater in its posterior half than in its anterior half. It will also be noted more clearly from this aspect that the hinder borders of the bothria project a considerable distance beyond the true anterior end of the strobila. Thus the length of the scolex is not that of the bothrium, as many writers have evidently taken it to be, but as far as can be determined from external views, more nearly that of the marginal sulcus plus an extension of the same to the tip of the scolex, or, where the latter is retracted, to the anterior border of the labia. The breadth of the scolex is here taken for the sake of convenience to be that of the bothrium, since there is very little difference between the two in this regard. The two apertures of the bothria are united over the tip of the scolex by a saddle-shaped groove, the edges of which are somewhat swollen so as to form lip-like structures. This groove has been described and figured for *C. crassiceps* by Molin (1861:235, Fig. 2, Tab. V) and Ariola (1900:397, Fig. 17, Taf. VIII) and figured by Linton (1901a:Fig. 267, Pl. 24), but it does not appear either in the figures given by Wagener (1854:Fig. 75, Taf. 7; 1857:Fig. 6, Pl. II) or that by Johnstone (1909:87, Fig. 14). It is present in all of the writer's material even to the youngest, but in a few cases the tip of the groove, that is the extreme tip of the scolex, is so prominent as to more or less obliterate the lips (Fig. 49). It is also to be noted that the lateral grooves separating the bothria do not pass thru these lips. This is nicely indicated in Ariola's figure but erroneously described by him as "passando per l'apice," and as further figured but in the same relation by Johnstone. Wagener's figure 75 and Linton's figure 266 also give the erroneous impression that this groove passes right over the tip of the scolex. Molin (1861:235), while giving a somewhat confused description of the relations between the saddle-shaped structures—which he figures as including the apertures of the bothria more posteriorly—and the lateral grooves, says that he saw in the apex an aperture which not only ended blindly but which was bounded by two eminences, simulating lips. This may have been due to extreme contraction of the tip of the scolex between the lips of this groove. It will be recalled that Leuckart (1819:46) stated in this connection that "An dem Kopfende ist eine kleine Vertiefung in der Mitte; die von den

beiden sich hier vereinigenden Randfurchen herrührt, wodurch ihre Ränder etwas erhabener werden. Die Grübchen sind kaum von der Grösse eines Nadelknöpfchens und tief in Kopfe, so dass es fast scheinen könnte, als wären sie wahre oscula;" but his figure 26, very good in other respects, does not do justice to his description of these terminal structures. Compare also Lönnberg's (1893: 15-17) *B. neglectus*, the figure for the scolex of which looks very much like *B. crassiceps*.

There is no neck in this species, but segmentation begins immediately behind the scolex (Fig. 48) and is complete thruout the strobila. These characters were included by Lühe (1899:44) in the diagnosis of the genus: "Aussere Gliederung vollkommen, ein gegliederter Hals fehlt." As regards this quotation, it would appear that the "gegliederter" is either superfluous or a *lapsus calami* for "ungegliederter." The anterior border of the first segment, a greater part of which is obscured by the hinder edges of the bothria, is constantly somewhat narrower than the latter, but its posterior border is usually about the same width even in such contracted specimens (Fig. 29). Its outline is somewhat trapezoidal, while its length is slightly greater than that of the segment immediately following. The breadth of this first segment varies anteriorly from 0.40 to 0.92mm. and posteriorly from 0.65 to 1.16—Linton's measurements are 0.78 and 1.07, respectively. Following this the segments are closely set, five to six times as broad as long, while their somewhat thickened posterior borders protrude on either side (as well as dorsoventrally) so as to give the strobila a serrate appearance (Fig. 48). It is here that the formation of new proglottides takes place by the subdivision of preexisting segments. This serrate appearance is also present in the posterior part of the strobila, where the proglottides are quadrate to twice as long as broad.

Posteriorly each serration does not necessarily define the posterior border of a proglottis. This is due to the presence of spurious articulations, possibly included in Wagener's "articulatio spuria." These are furrows which arise laterally, where they do not stand out as distinctly, however, as the true posterior borders of the proglottides, but do not pass to the median line. They are not present in all of the posterior proglottides nor are they symmetrically arranged. In the following excerpt from his more complete diagnosis it is to be seen that Rudolphi (1819:477) did not refer to these structures:

"Articuli breves, margine posteriore incrassato utrinque exstante, quo corpus serratum fiat. Articuli ceterum inaequales, ut passim augustiores et longiores intercurrant." F. S. Leuckart said only, "Die ersten Glieder am Kopfe schmaler als die Übrigen, dann folgen fast gleichbreite, die letzte Hälfte der Glieder breiter als lang, mit deutlichen, weissen Ovarien," which statement refers to "der beschreibene nicht ganze Wurm . . . 1½" lang." Diesing (1863:236) described the strobila as " . . . ellipticum, articulis ad medium usque increscentibus, inde descrescentibus, marginalibus posticis utrinque prominentibus, articulo singulo plica transversali diviso . . . " The latter has reference obviously to Wagener's "articulo spuria." It is also seen that, as regards the shape of the strobila, he

(Diesing) was dealing with much contracted specimens, the length being cited as ranging from one and a half lines to two inches. Ariola (1900:397) gave the following description of the segments:

"Strobila anteriormente assai piu stretto dello scolice, a guisa di peduncolo; le primi proglottidi sono rettangulari, strette, ma rapidamente si allargano; raggiunta la massima dimensione, la conservano sino all ultimo tratto del corpo, dove nuovamente si restringono. Le proglottidi mature hanno angula posteriori appena visibili; le ultime presentano forma trapezoidale." And Johnstone (1909:89) stated, "The posterior proglottides are much broader (in the transverse axis of the strobila) than they are long (in the longitudinal axis of the strobila); and their anterior extremities are narrower than the posterior ones, so that the edge of the strobila appears to be serrated. Secondary segmentation of the proglottis often occurs."

In fine, Wagener, Diesing, and Johnstone are, to the writer's knowledge, the only writers who have referred to this spurious articulation or subdivision of the segments into false secondary segments—although Lühe (1902:629) repeated the statements of the first two authors. Furthermore, Wagener did not figure the adult strobila of the species to show the structures in question, but in the legend for his figure 79, Taf. 7 of *Dibothrium heteropleurum*,—now *Amphicotyle heteropleura* (Diesing)—says only that "Man sieht die articulo spurio, welche die echten Glieder, wie bei *Dibothrium crassiceps*, in der Mitte theilt"; and further, as regards the difference in structure of the sides of this species, "Der Schein entsteht durch die noch dichtere Zusammendrangung der Falten der wahren und falschen Glieder auf der concaven Seite." In the legend (p. 61) for his figure 6, the egg of *C. crassiceps*, he also said that "Jedes Glied hat in der Mitte eine Falte, die ihm das Ansehen giebt, als bestunde es aus zwei Gliedern." Thus, there is reason to believe that for this species no one (apart from Linton's Fig. 268) has as yet described nor figured what the writer here calls spurious articulations, but that these workers were referring to the secondary division of the segments of the anterior end of the strobila which proceeds in the manner described for *B. scorpii* et al., altho not so clearly (Figs. 48 and 58). This is borne out by the fact that the spurious articulations described here never reach the median line of the strobila, much less pass completely across it as do the true posterior borders of the proglottides (Fig. 74). In one moderately relaxed strobila the first segment showing spurious articulations appeared 11.7mm. from the tip of the scolex, while in another which was quite contracted, especially anteriorly, 4.8mm. In the former case the next two pairs of these structures—and all of these in question happened to be bilaterally symmetrically situated—appeared in the fourth and thirteenth segments following.

Posteriorly the uterus-sacs appear as a series of gradually enlarging, dark punctations, as described below, not so pronounced, however, as in *B. scorpii*. The measurements of the first proglottis showing eggs in the uterus-sac in a fairly relaxed strobila at hand were 0.50mm. in length by 0.92 in breadth, while for one farther back where the uterus-sac was 0.61 by 0.48

mm., they were 1.31mm. in length by 0.82 in width. These measurements are, however, of only relative value. Another strobila of the same age but contracted at the time of fixation might show the same regions more like those farther ahead and, thus, in alcoholic specimens, evidently younger.

The following table gives various external measurements of six specimens in alcohol for the purpose of comparison; all dimensions are in millimeters.

Length in mm.	87	92	43	Little more than scolex	29	72
Length of scolex (lateral view)	0.87	0.59	0.46	0.43	0.63	0.83
Length of bothrium	1.08	0.77	0.64	0.64	1.00	1.01
Breadth of same	0.75	0.57	0.52	0.53	0.67	0.90
Thickness of same	0.87	0.64	0.68	0.58	0.74	1.21
Breadth of segment I, anteriorly	Much contracted	0.40	0.37	.....	0.55	0.92
Breadth of same, posteriorly	Ditto	0.53	0.60	0.53	0.74	1.16
Thickness of same, posteriorly	0.37	0.38	0.24	0.27	0.52	.....
Maximum breadth in anterior part of strobila	1.01	0.82	1.06	.....	1.30	.....
Same in posterior part of strobila	1.11	1.04	1.16	....	1.48	1.38

The cuticula varies in thickness from 2 to 5μ, the most common measurement being about 2.6μ. Resting on a distinct basement membrane, well shown after the use of Mallory's stain, it is divided into two strata of equal thickness by a granular layer, the components of which seem to be related to the bases of the stout, somewhat club-shaped pseudocilia or "hairs" which constitute the outer moiety. While the inner stratum was found to be homogeneous with the stains used, the outer showed two intensities of color, an inner lighter and an outer darker. The former represents the narrowed central ends of the spindle- or club-shaped pseudocilia, while the latter is determined by the well-stained bodies of the cirri themselves. Linton (1901:473) said that "the cuticula is covered with minute spines," but Johnstone (1909:89) said, concerning these structures: "I can see nothing of this kind in the species before me." All over the scolex and in the form of a band on the posterior borders of the proglottides (Fig. 103) these cirri become modified into stouter spinelets from two or three times longer than elsewhere and everywhere directed posteriorly, quite like those described by the writer (1914a:85) for *Haplobothrium globuliforme*, but much longer relatively; thus indicating their function as accessory organs of attachment. The largest spinelets are in the middle of this band, those at the edges, that is in the anteroposterior direction, gradual-

ly merging in length into the pseudocilia of the cuticula of the neighborhood. Furthermore they are arranged in the same manner on the posterior borders of the spurious articulations and of all of the secondary segments situated in the anterior portion of the strobila. They were referred to by Wagener (1854: 5), Diesing (1863:236) as "articulo singulo . . . postice ciliis instructo," Cohn (1902:55) and by Lühe (1902:238, 247) who considered "dass es sich nicht um in die Cuticula eingesenkte Stacheln handelt, wie bei dem Stachelkleide so vieler Distomen, sondern nur am Fortsätze der Cuticula, durchaus analog denjenigen, welche Looss an der bereits oben citierten Stelle fur *Haematoloechus asper* abgebildet hat."

The subcuticula, about 20μ in thickness, consists of fairly elongated cells, the nuclei of which are situated at their central ends close to the vitelline follicles. Their boundaries are difficult to ascertain, the whole layer thus being more of the nature of a syncitium. For about one-third of their length immediately beneath the cuticula the cytoplasm becomes broken up into a number of more or less parallel processes which stand out in distinct contrast with the deeper inner ends of the cells, especially in transverse sections.

The parenchyma, everywhere encroached upon by the voluminous reproductive organs, is in the form of a comparatively open reticulum showing no features of special interest. It is naturally most abundant in the posterior flared ends of the proglottides. In small strobilas it is more compact in structure and contains relatively more nuclei. Distinct spaces, formerly occupied by calcareous bodies, such as are readily and distinctly seen in the parenchyma of *B. scorpii*, were found neither in the scolex nor in the strobila; nor were these structures noticed in living material.

The musculature is composed of the typical three sets of fibres, interfered with in the usual manner by the large reproductive organs and their external openings. The sagittal and frontal series are only moderately developed, while the longitudinal series is about 10μ in thickness and situated within the frontal series. Its fibres are arranged in bundles of irregular shape (in cross-section) and width but of this uniform thickness, excepting where they are naturally much flattened out dorsally and ventrally by the distended uterus-sac. They are also continuous from joint to joint. A very weakly developed series of outer longitudinal muscles is present, while the muscles of the posterior border of the proglottis (vide Lühe 1897a) are poorly developed, in fact even less so than in Bothriocephalus.

In the scolex the frontal fibres are better developed than the sagittal ones, and pass around the bothrium closer to its lumen than to its external surface, while the latter are mostly confined to the region between the bothria. The inner longitudinal muscles of the strobila pass forward into the scolex, dividing as they meet the lumina of the bothria to pass around them and attach themselves to the margins of the apertures. They are thus directed somewhat obliquely as shown in Johnstone's figure 18 and described as ". . . running irregularly, probably obliquely, round the walls of the bothrium. These no doubt function as constrictors of the latter." A few pass on forward to the

tip of the scolex to assist in activating that region. Between the bothria, however, they were found to be separated into dorsal and ventral layers as in the strobila, and not united into a single coronal band, as shown by Johnstone. The bothrial sphincter (Fig. 48) is a powerful bundle of fibres, about 0.07mm. in transverse section surrounding the aperture close to its cuticula. In transverse sections of the scolex it appears as a deeply staining mass on each side of the opening, also shown in Johnstone's figure 15. As it crosses the aperture anteriorly it becomes greatly attenuated. This with its comparatively great size at the sides and posteriorly accounts for the almost complete disappearance of the aperture in many adult, preserved scolices owing to the powerful contraction of this muscle from behind forward, thus diminishing the opening towards the tip of the scolex. From their arrangement it is to be seen that this sphincter, evidently a modified group of frontal fibres, and the longitudinal muscles in the scolex play a more important role in the movements of the bothria than do the other groups. On account of their oblique course the longitudinal fibres evidently act in diminishing the size of the lumen of the bothrium as well as do the circular frontal fibres of the latter.

The nervous system consists of two longitudinal strands which enlarge in tip of the scolex to form two somewhat elongated ganglia. The latter are united by only a few fibres, but they send out comparatively large nerves to the bothria. In the strobila the chief strands, each from 15 to 20μ in diameter, are situated ventrally in the medullary parenchyma, just within the longitudinal muscles and from one-fifth to one-quarter the width of the strobila from its lateral margins (Fig. 90). About halfway along the scolex the strands are about 80μ in diameter; but the ganglia are somewhat smaller and situated close together about 0.15mm. from the summit. In other words the chief strands enlarge and diverge gradually until the equatorial region of the scolex is reached and then diminish in size as they converge to form the ganglia. A pair of prominent nerves is sent forward on each side to supply the saddle-shaped groove described above. In young strobilas the nerve strands are situated midway between the dorsal and ventral surfaces, and not ventrally.

The excretory system consists of a pair of longitudinal vessels, situated ventrally, that is, in the same frontal plane as the chief nerve strands, each vessel being in the anterior end of the strobila about halfway between the nerve strand and the median row of reproductive rudiments. These vessels break up in a very irregular manner into extremely elongated loops, so that for considerable stretches four vessels will appear while again the branchings will be so numerous as to make it very difficult to decide, on looking at a transverse section, which are the main channels (Fig. 48). In other individuals four vessels appear, so that one is led to conclude that the pair just mentioned represent the latter, fused at times but separated again to form the loops. But whether these four vessels represent the typical four of other orders is a matter of conjecture. These main vessels may continue back into the ripe joints close alongside the uterus-sacs, but they usually break up into a very diffuse reticulum throughout the medullary parenchyma in the region where the openings

of the cirrus and vagina pierce the cuticula in development. Behind this region it was found impossible to trace the main vessels with satisfaction. The system usually passes into the scolex as two vessels, but soon breaks up into an elaborate net-work which ramifies between the bothria and throughout their walls. These branches are shown in Johnstone's figure 15. As regards the conditions of the excretory system in the extreme posterior end of the strobila, the material at hand permits of only negative conclusions. In the youngest strobilas, such as that shown in figure 49, the vessels converge posteriorly to open into a notch in the cuticula, there being no definite terminal vesicle such as is present in plerocercoids of the genus Proteocephalus, for instance. From this and the further fact that Wagener (1857:93) showed (Fig. 6, Pl. II) the main vessels in a very small strobila, which he examined while it was alive, passing separately to the outside, one is led to conclude that the vesicle, if ever present, must have been situated in the walls of an enveloping cyst and disappeared with the latter as in the Trypanorhyncha or the Cyclophyllidea. This seems to have been Wagener's idea of the situation when under his figure 65 (1854:68) he said: "Man sieht keinen pulsirenden Schlauch am spitzen Schwanzende. Es muss dies Thier auf ähnliche Weise entstanden sein, wie das in Fig. 74 dargestellte," and figure 74 is that of "Dibothrium (Belones ?)" from *Scyllium canicula* enclosed in a cyst in the walls of which "man sieht die Gefässe der Cestodenblase."

The earliest reference to the genitalia of *C. crassiceps* was by Rudolphi (1819:477) who said:

"Ova vel ovalia vel ovata, forsan secundun majorem maturitatis gradum. A B. punctato diversissimus, licet ovaria lateralia fuscescant, sed haec ipsa etiam in B. crassicipite quam in B. punctato majora sunt."

The structures called ovaria were evidently the uterus-sacs. F. S. Leuckart (1819:46) described the reproductive organs of his *B. pilula* as follows: ". . . die letzte Hälfte der Glieder breiter als lang, mit deutlichen, weissen ovarien. An den unteren Gliedern sieht man oberhalb jedes Eierstockes einen wasserhellen Punkt, wahrscheinlich Oeffnung fur das mannliches Zeugungsglied." From a comparison of this with his description and figure of posterior proglottides of *B. scorpii*, it is evident that he too was dealing with the uteri and their openings, respectively. He also referred to ". . . den schwarzen Punkten des Körpers, die Rudolphi fur Ovarien gehalten" of Redi's worm, which Rudolphi called (1810:67) *Bothriocephalus gadi merluccii* and placed in his "Species dubiae." Wagener (1854a:61) said that "Die Eier häufen sich in obersten Theile der Glieder an. Der Dotterstock verzweigt sich uber das ganze Glied und liegt overhalb der vescicules transparentes van Beneden. Die Geschlechtsöffnung ist in der Mitte und lateral." Diesing (1863:236) placed the "Aperturae genitalium laterales in linea mediana." Ariola (1896:265-266) gave the first comprehensive description of the reproductive organs in the following words:

"Tuttaria sul corpo si osservano macchie scure molto sporgenti, constituite della massa die uova. Tali rilievi non sono propriamente, nella linea mediana,

ma collocati a destra o a sinistra die essa formando in tal modo une striccia a zig-zag.

L'aperture genitale maschile sbocca sulla faccia dorsale, e sulle opposta si apre l'utero. In alcune proglottidi l'ovario e bilobo, la uova sono ellissoidali e mancano di operculo."

Lühe (1899:42-44) in defining the characters of the genus gave the general features of the genitalia, while Ariola (1900:397) enlarged his own 1896 description: "Ovario con numerose uova, talora bilobo; uova ellissoidali aventi nel diametro longitudinale 67μ e nel trasversale 32. . . ." Braun (1900) reviewed the literature on the genus and species up to date, and Volz (1900) discussed the reproductive organs of the species as compared with those of his *B. spiraliceps* and the position of the openings in connection with brief remarks on the phylogeny of the genus *Bothriocephalus* s. lat. As regards his own specimens Linton (1901:473) said that "Posterior segments show rudiments only of the reproductive organs, but no indication of external genital openings." And later Johnstone (p. 89) remarked that "the genital openings are in the middle line of the proglottides but near the anterior borders of the latter," referring evidently, as will be seen later, to the uterine openings only.

The rudiments of the reproductive organs appear about three millimetres from the tip of the scolex as aggregations of nuclei that can just be discerned in toto mounts (Fig. 48). About three millimetres farther posteriorly in moderately contracted older strobilas (such as would be obtained if no special care were taken during the fixation of the material) the cirrus and vagina are seen to be just piercing the dorsal surface. Before this region is reached, however, the common rudiment, at first circular and then elongated oval in outline, differentiates into a more anterior portion, the rudiment of the whole uterus, a more posterior less elongated part, the beginnings of the cirrus-pouch and vagina, and a third, connecting the other two near the hinder edge of the proglottis, the nuclear aggregation that will develop into the ovaries and the organs of the interovarial space (Fig. 74). As mentioned in the specific diagnosis, the first two of these rudiments alternate irregularly from side to side as do the corresponding adult structures. At the same time the testes and vitelline glands are developing in the medullary and cortical portions of the parenchyma, respectively.

A distinct genital sinus or cloaca, the opening of which is usually almost circular in outline, is present (Fig. 75). It varies from 0.05 to 0.09mm. in diameter and is situated, as above noted, nearly in the median line, dorsally, and from three-fourths to one-half the length of the proglottis from its anterior border, usually just posterior to the spurious articulations when they are present. At the bottom of this sinus there is a secondary cloaca ("Geschlechstasche" or "Ductus hermaphroditious"), also circular in outline, from 15 to 25μ in diameter, and into it open the cirrus and vagina quite close together, the latter immediately behind the former. This secondary sinus is best seen in sagittal sections (Fig. 103). The genital pore (the opening of the main sinus) is elevated slightly above the general dorsal surface of the proglottis,

thus appearing as a low cone or crater. No sphincters control the openings of either of these sinuses but the cuticula of the floor of the larger or outer is modified to form coarse, low, rounded and closely set papillae which are evidently of special importance during copulation. These papillae would evidently serve to temporarily fasten the structure into the primary sinus of another proglottis, when it is possibly everted with the cirrus. Copulation was not observed in this species during life, nor were any cases of protruded cirrus met with in the material at hand.

All of the proximal portions of the reproductive organs, excepting the vitelline follicles, are located in the medullary parenchyma, although the much distended uterus-sac, originally in the latter, extends almost to the cuticula on both the dorsal and ventral surfaces. Figure 75 shows their arrangement in toto.

The testes are closely arranged in the medullary parenchyma in two lateral fields, each bounded laterally by the junctions of the dorsal and ventral layers of longitudinal muscles and medially by the other reproductive organs (excepting the vitelline glands) which occupy in the quadrate proglottides about the middle one-third of the transverse diameter of the strobila and are contiguous from joint to joint. In the quite mature elongated proglottides the testes are ellipsoidal in shape, averaging 0.125mm. in length by 0.040 in diameter, the cross-section being usually about circular in outline. In younger joints and in all those of much contracted strobilas the testes are nearly spherical in shape, measuring about 60μ in diameter, or often slightly longer than broad. They are arranged in a single layer in the medulla, the whole dorsoventral diameter of which they occupy, and are continuous from proglottis to proglottis. From 2 to 4 appear in each lateral field in transverse sections, from 5 to 7 are seen in sagittal sections between the posterior borders of consecutive proglottides, while, so far as could be determined from frontal series directly, the number is from 20 to 25. Thus each proglottis contains from 40 to 50 testes.

The vas deferens forms a wedge-shaped mass of closely arranged coils, extending forward immediately ahead of the cirrus-pouch and alongside the uterus-sac for about two-thirds of its length (Fig. 75). In proglottides in which the latter is yet comparatively small the vas deferens may pass forward as far as its anterior end. In either case it forms with the cirrus-pouch a mass which alternates from right to left with the uterus-sac. When distended with sperms the duct averages about 30μ in diameter; but just before it enters the cirrus-sac anterodorsally it narrows down to 5μ. Immediately within the wall of the latter it often enlarges again to form a thin-walled functional vesicula seminalis, or perhaps more correctly ductus ejaculatorius, from 13 to 23μ in diameter. After one or two short turns it diminishes again to about 8μ and then passes on as the cirrus proper. While the proximal portions of the duct do not pass in any definite direction, the latter is situated for most of its length in the longitudinal axis of the pouch. It is about 0.10mm. in length and about 20 to 25μ in diameter at its middle. It is lined with a cuticula, 10μ thick, which is cleft but not armed with bristles of any kind.

The cirrus-sac (Fig. 103), situated immediately behind the uterus sac or lateral to its posterior end, is elliptical to slightly oval in outline, and measures 0.128 to 0.162mm. long, 0.087 to 0.116 wide and 0.098 to 0.116 deep. The longitudinal axis is directed anterodorsally from the genital sinus and to the right or left, according as it alternates with the uterus-sac. The proximal one-third of the contents of the pouch consists of loose parenchymatous tissue with a few muscle fibres surrounding the ductus ejaculatorius, while the distal two-thirds, that part which accommodates the cirrus proper, is supplied mostly with muscles which actuate the latter. Large fibres proceed somewhat obliquely from the wall towards the proximal pole of the sac to become broken up or frayed before they are attached to the cirrus tangentially, so as to give the appearance in frontal sections of the latter being surrounded by a comparatively heavy layer of fine lightly staining circular fibres. A few of the fibres closest to the cuticula of the cirrus were considered to be true circular fibres; but no longitudinal fibres were seen. The wall of the cirrus-sac is from 2 to 3μ thick and is made up of very fine closely matted fibres, the direction of which could not be determined with satisfaction. The sac lies freely in the parenchyma of the region and is not connected by any special muscles to the dorsal or ventral body-walls; nor are the body muscles attached to it as in some cestodes. The layers of the latter are simply pierced and the fibres turned aside in evidently a passive manner.

The opening of the vagina is close behind that of the cirrus at the bottom of the secondary genital sinus, or as it has been called by Fuhrmann, "ductus hermaphroditicus" (Fig. 103). From this point the duct courses ventroposteriorly in the mid-line and then parallel to the dorsal surface of the proglottis until it reaches the ovarian isthmus, above which it makes a few turns and quickly diminishes from 20μ in diameter half way along its course to 10μ. It then dips farther down into the genital space, often enlarging slightly as it does, and soon joins the oviduct at an enlargement of the latter situated a short distance behind the oocapt. Throughout its length it is lined with a ragged or pseudociliated cuticula and surrounded by radially arranged nuclei connected with the cuticula by cytoplasmic strands like those described by the writer for *H. globuliforme* (1914a:105) and considered to be possibly extruded nuclei of the original epithelium as well as the myoblastic nuclei of circular fibres, a layer of which surrounds the duct. There is no vaginal sphincter.

In his generic diagnosis Lühe states that the receptaculum seminis is small and in his description of the family Ptychobothriidae (1902:327) says that when present it is "in Gestalt eines kleinen Blindsäckchens ausgebildet, welches parallel neben dem Endabschnitte des Oviduktes liegt and mit der Vagina unmittelbar vor deren Vereinigung mit dem Ovidukt in Vergindung steht." On the contrary it was found to be a comparatively large structure but very difficult to orient in sections made in any direction. It is in the form of a thin-walled sac about 60 by 20μ, wrapped somewhat spirally around the dorsal wall of the above-mentioned enlargement of the oviduct and opening by an

aperture equal to its whole diameter into the vagina just at its juncture with this vestibule. But since the vagina constantly constricts a second time to a diameter of about 8μ before entering the latter, one gets the impression of the receptaculum seminis being a diverticulum of the oviduct rather than of the vagina. Figure 108 of four consecutive sections of a transverse series, showing the union of these ducts, will give a better idea, perhaps, of the nature of the seminal receptacle.

In mature proglottides the ovary (Fig. 90) is a bilobed structure situated in the median line, close to the posterior border of the proglottis and immediately ahead of the uterus-sac of the proglottis following, where the latter is much distended with eggs (Fig. 75). In toto mounts the lobes seem to be quite separate from each other, but in sections the isthmus is easily made out. It occupies the ventral half of the medulla while the wings or lobes extend completely across the space between the layers of longitudinal body muscles. The lobes are about 0.27mm. long by 0.13 wide, while the isthmus is 0.06 to 0.08mm. in anteroposterior diameter. These proportions are, however, much different in much contracted strobilas or in proglottides in which the uterus-sac is distended with eggs. In both instances the ovary is very much flattened anteroposteriorly and, in the latter case, all but obliterated, as shown in Lühe's figure 8 (1902:326). The ova from that portion of the isthmus where they are ready to be passed on by the oocapt, are elliptical to oval in outline in sections and measure on the average 18 by 10μ, their nuclei being about 9μ in diameter.

The oocapt, situated in the median line at the posterior border of the ovarian isthmus, somewhat dorsally, is a spherical to ovoid muscular organ about 20μ in diameter (Fig. 103). Immediately behind it the oviduct constricts to a diameter of only 7 to 10μ and then passes on posteriorly and ventrally either to the right or to the left, gradually enlarging until the above-mentioned vestibule is reached, when the diameter is 25 to 30μ. The latter enlargement is less of the nature of a direct continuation of the oviduct than a more or less separate thin-walled structure—the walls of the oviduct up to this point being comparatively thick (Fig. 108)—into which the oviduct opens by a slightly elongated aperture. While the wall of the first portion of the oviduct consists of more or less cubical ciliated cells with somewhat indefinite boundaries—ordinarily they stain very densely—that of the vestibule shows only a few scattered nuclei protruding into the lumen. The oviduct continues posterolaterally and ventrally from one corner of the vestibule (that with which the vagina is usually connected) as a tube quickly diminishing from 15 to 10μ in diameter and lined with a ciliated epithelium with prominent nuclei but no distinct cell-boundaries. Close to the anterior wall of the uterus-sac of the succeeding proglottis it turns upward sharply and at about the middle of the dorsoventral diameter of the medulla takes on the vitelline duct. It then skirts the uterus-sac, just mentioned, as it passes to the opposite side of the generative space and slightly forward, to soon become surrounded by the shell-gland.

The vitelline duct at its union with the oviduct has a diameter of 8μ; but just beyond this, in the direction of the follicles, it soon enlarges to form a somewhat irregular vitelline reservoir which when filled with yolk may attain a diameter of 30μ. Its general course is towards the opposite side of the generative space almost parallel to either surface of the body; but beyond this it could not be traced with satisfaction.

The vitelline follicles fill up almost the whole of the cortical parenchyma from the layer of longitudinal body muscles to the nuclei of the subcuticula, the thickness of the stratum averaging 0.05mm. (Fig. 90). They form a continuous layer around the margins of the proglottides (in transverse sections) and also from proglottis to proglottis, as mentioned above, even extending well into the posterior borders. They are not arranged in lateral fields, but are interrupted only where the uterus sac and genital sinus pierce the body-wall, or in the former case greatly press against the latter. The individual follicles attain a size of 60μ and are very closely crowded together. The number in cross-sections of the proglottis averages 55 and in sagittal sections 13, thus making the average total number for each proglottis 715.

The shell-gland is situated in the dorsal portion of the genital space, that part of the oviduct showing the connections being almost horizontal in position and about 18μ in diameter, that is, a little larger than the oviduct behind that region. The individual cells of the gland are much attenuated, closely arranged and have their nuclei situated in their slightly enlarged distal ends. Their connections with the oviduct give the wall of the latter a honeycombed appearance when it is seen in longitudinal section.

Beyond this region the oviduct gradually enlarges as it passes above the ovarian isthmus to become the uterine tube, the coils of which are accommodated opposite the cirrus pouch just behind the uterus-sac. As it proceeds its wall gets thinner and the nuclei protrude more and more into the lumen until many of them are evidently lost. It is noteworthy that the uterine tube in many cases as well as the uterus-sac, especially in younger proglottides, alternates irregularly from right to left according as the cirrus and vas deferens do. These three structures are, in fact, fitted very nicely into the space between the uterus-sac ahead and the ovarian isthmus behind.

The uterus-sac is elliptical in outline, has its longitudinal axis directed anteroposteriorly, and is situated in the anterior half of the proglottis. In very mature segments it occupies almost the whole of the medullary region, or to be more precise, the middle three-fifths of the diameter of the proglottis, its anterior end extending forward close to the ovary of the proglottis immediately ahead (Fig. 75). Lühe (1902a:326) figured the uterus as, to use his own words, " . . . in der Regel eine geräumige Uterushöhle bildend, welche die übrigen Genitalorgane, ohne dass freilich deren Rückbildung eintritt, buchstäblich an die Wand drängen kann, indem die ganze Proglottis in reifen Proglottiden vielfach als ein einziger sackförmiger Eibehalter mit verhältnissmässig sehr dünnen Wandungen erscheint." But such a degree of restriction of the other genitalia was seen by the writer only in a few of the ripe proglottides of strobilas

much contracted longitudinally. There the largest uterus-sac measured 0.8mm. wide by 0.67 long, while the width of the proglottis in question was, at the posterior borders of the spurious articulations, 1.57mm. In fairly relaxed strobilas it increases in dimensions from 0.18 by 0.14mm., where the first eggs appear in the lumen, to 0.87mm. long by 0.48mm. wide, where the proglottis is 0.80mm. wide at its middle, in the latter case, of course, pressing against the dorsal and ventral walls even as far as the cuticula. From a comparison of these measurements, and the further fact that in the case of the former much contracted strobilas there often appears, behind the region showing the nearly obliterated genitalia, a more relaxed one in which the relations of the uterus-sac to the other organs is quite as in the competely relaxed strobilas, one is inclined to conclude that the characters of the family above quoted apply to this species only in the case of proglottides much contracted longitudinally. In the quadrate proglottides the smaller, that is, younger sacs alternate irregularly from right to left, as do the uterine openings, and according as the cirrus pouch and the vas deferens in particular (on account of its above-mentioned position) occupy the opposite sides of the proglottis. Externally, in alcoholic specimens, the uteri appear as a gradually enlarging series of brown punctations caused by the contained eggs showing through the thinned body wall, as pointed out originally by Rudolphi and other writers.

The wall of the uterus consists of a thin membrane on the inside of which a very few scattered and somewhat flattened nuclei indicate its original epithelial nature. In young proglottides, where no eggs are to be seen in the small uterine cavities, the wall is composed of an epithelium about 8μ thick, showing prominent nuclei but no distinct cell-boundaries. Furthermore in such early stages the lumina of the uterine ducts, developing in the manner described by Young (1913) and Shaefer (1913), are not completely formed nor in connection with the cavities of the sacs, but the uterine apertures are prominent. In the first two or three sections of a 10μ frontal series, taken from the ventral surface, they appear as distinct somewhat elliptical apertures about 26μ in transverse diameter, but in the third or fourth section are closed, only to reopen as the cavity of the uterus-sac, thus showing that the membrane closing the aperture is only about 10μ in thickness. And this closed condition is maintained until the uterus-sac attains the above-mentioned maximum size and becomes greatly distended with eggs. Then the functional opening is established by the rupture of the membrane which has meanwhile reached a length of 0.046 to 0.058mm. by a width of 0.034 to 0.046, its elliptical outline thus having been retained. The opening does not become as regular in outline, however, as the membrane, for the latter remains around the rim as ragged processes, which render the determination of the exact location of the aperture in toto mounts a matter of no little difficulty. The uterus opening is surrounded by a series of radiating cells like those of the opening of *B. scorpii* described above.

The fresh eggs examined in saline solution are elliptical to ovoid in shape, 75 by 40μ in dimensions and provided with a thin, very light brown shell hav-

ing no operculum. The color is so faint that it can be seen to advantage only when the eggs are in masses or in the uterus-sac. Ariola (1900:397) gave the measurements of the eggs of the European species as 67 by 32μ. The largest examined were immature, the contents consisting of large spherical cells only, like those shown by Wagener (1854a) in his figure 6, Taf. I. When the worms are still attached to the wall of the intestine of the host between the mucous folds, they often discharge many of their eggs from most of the posterior proglottides when their scolices are irritated with a blunt needle in order to make them loosen their comparatively firm hold.

Forty-four specimens of *Merluccius bilinearis* were examined at Woods Hole and at Harpswell, but no definite idea of a possible intermediate host was obtained. It was noticed, however, that when the intestine of the fish contained much grey chyle, presumably the result of the digestion of small herring—definitely ascertained at South Harpswell to be such in a few cases-and of *Pomolobus aestivalis* (Mitchill), the blueback—no tape-worms of this species were present; but where amphipoda were found in the stomach or the remains of such in the intestine the worm was plentiful. Furthermore, where nothing was found in either stomach or intestines, other than yellowish chyle in the latter—as in most fish examined—indicating amphipods and other small crustaceans as food rather than small herring, the worm was also common. All stages from the youngest strobilas, such as that shown in figure 49, to the oldest were found, but none nor any plerocercoids were met with in the course of the thoro dissection of the available stomach contents of the hosts, both fish and crustaceans. In a number of cases, nevertheless, only very young strobilas were found in the intestine of the host, thus pointing to possible sudden infections at different times. Wagener, who figured the youngest strobila that has yet been recorded, in fact nothing much more than the scolex, said nothing more concerning the life history than that, on account of the excretory vessels opening separately to the exterior in this very young specimen, there might possibly have been a vesicular appendage to the larva in the nature of an enveloping cyst comparable to that described and figure for "Dibothrium (Belones?)" from *Scyllium canicula*, concerning which he said (l.c., p. 45): "Vergleicht man diese Form vom Cysticercus mit den vorigen [*Cysticercus fascicolaris* Rud.], so ergiebt sich, das der Unterschied nur in dem Aufhängebeutel sich findet, der Kopf und Blase verbindet."

A detailed description of the species is here given, not only because it is evidently the only one belonging to the genus, but because descriptive details are so lacking from the European literature that the determination of the species is attended with considerable uncertainty. The writer, however, considers that, on the basis of the published accounts and reports of the species, but in the absence of European material for comparison, the form occurring on this side of the Atlantic Ocean must be looked upon as identical with the *C. crassiceps* of Europe.

The material studied consisted of No. 204, 259, 261, 262, 269, and 282 in the writer's collection from the intestine of *Merluccius bilinearis* as above listed.

AMPHICOTYLINAE Lühe 1902

Scolex with two typical, usually not very deep bothria, which in some forms develop posterior, sucker-like portions. In an isolated case a pseudoscolex is substituted for the scolex. External segmentation insignificant, at times disappearing thru accessory wrinkling or folding of the surfaces of the proglottides. Opening of cirrus and vaginal marginal, irregularly alternating, with more or less strongly pronounced tendency to unilaterality. Uterus-opening median; uterus-sac always well developed. Coiling of vas deferens strongly expressed.

Occurrence: In fishes.

Type genus: Amphicotyle (Diesing 1864) Ariola 1900, e.p. Lühe 1902.

ABOTHRIUM van Beneden 1871, char. emend. Lühe 1899

Taenia (part.)	Auctorum	
Rhytis (part.)	Zeder	1803
Bothriocephalus (part.)	Rudolphi	1809
Bothriocephalus (part.)	Rudolphi	1819
Bothriocephalus (part.)	Leuckart	1819
Dibothrium (part.)	Diesing	1850
Bothriocephalus (part.)	Baird	1853
Dibothrium (part.)	Diesing	1863
Bothriocephalus (part.)	Olsson	1867
Abothrium	Beneden	1871
Abothrium	Moniez	1881
Dibothrium (part.)	Linton	1890
Abothrium	Lönnberg	1891
Bothriocephalus (part.)	Matz	1892
Bothriotaenia (part.)	Ariola	1896
Bothriotaenia (part.)	Riggenbach	1896
Abothrium	Lühe	1899
Bothriotaenia (part.)	Ariola	1900
Abothrium	Lühe	1900
Abothrium	Lühe	1910

Scolex not exceptionally elongated, with two powerful but not especially deep bothria. Segmentation in older portions of the strobila usually insignificant on account of superficial wrinkling of the individual proglottides; ripe proglottides essentially broader than long. Longitudinal nerves near the lateral borders, dorsal to the cirrus-sac and vagina. Testes exclusively between the nerve strands. Vitelline follicles of very irregular shape, in two broad lateral fields, in part at least between the bundles of the longitudinal muscles, the follicles of individual proglottides not especially separated from one another. Ovary scarcely lobed, more or less bean- or kidney-shaped. Shell-gland dorsal to the ovary. Uterus-sac in ripe proglottides occupying the whole of the medullary parenchyma. The openings of the uteri correspond to a more or less prominent median longitudinal furrow of the chain of proglottides.

Type species: *A. rugosum* (Batsch).

ABOTHRIUM RUGOSUM (Batsch 1786)

[Figs. 32–36, 63, 76, 91, 109]

1773	*Taenia decimpollicaris*	Strussenfelt	1773 : 27
1781	*Taenia tetragonoceps* (part.)	Pallas	1781 : 88
1782	"Der runzlichter Fischbandwurm"	Goeze	1782 : 410
1786	*Taenia rugosa*	Batsch	1786 : 208
1788	*Taenia tetragonoceps* (part.)	Schrank	1788 : 46
1790	*Taenia rugosa*	Gmelin	1790 : 3078
1802	*Taenia rugosa*	Rudolphi	1802 : 107
1803	*Rhytis conoceps*	Zeder	1803 : 292
1810	*Bothriocephalus rugosus*	Rudolphi	1810 : 42
1816	*Bothrioceophalus rugosus*	Lamarck	1816 : 168
1819	*Bothriocephalus rugosus*	Rudolphi	1819 : 137
1819	*Bothriocephalus rugosus*	Leuckart	1819 : 57
1845	*Bothriocephalus rugosus*	Dujardin	1845 : 618
1850	*Dibothrium rugosum*	Diesing	1850 : 591
1853	*Bothriocephalus rugosus*	Baird	1853 : 88
1863	*Dibothrium rugosum*	Diesing	1863 : 239
1867	*Bothriocephalus rugosus*	Olsson	1867 : 53
1871	*Abothrium gadi*	Van Beneden	1871 : 56
1881	*Abothrium gadi*	Moniez	1881 : 167
1889	*Bothriocephalus rugosus*	Linstow	1889 : 242
1889	*Bothriocephalus rugosus*	Monticelli	1889 : 68
1890	*Dibothrium rugosum*	Linton	1890 : 750
1890	*Abothrium rugosum*	Lönnberg	1890 : 22
1891	*Abothrium rugosum*	Lönnberg	1891 : 75
1892	*Bothriocephalus rugosus*	Matz	1892 : 113
1894	*Bothriotaenia rugosa*	Blanchard	1894 : 701
1896	*Bothriotaenia rugosa*	Ariola	1896 : 280
1896	*Bothriotaenia rugosa*	Riggenbach	1896 : 223, 228
1898	*Bothriotaenia rugosa*	Muehling	1898 : 35
1899	*Abothrium rugosum*	Lühe	1899 : 39
1900	*Bothriotaenia rugosa*	Ariola	1900 : 432
1900	*Abothrium rugosum*	Lühe	1900a : 101
1901	*Dibothrium rugosum*	Linton	1901 : 412, 476
1903	*Bothriotaenia rugosa*	Schneider	1903 : 7
1910	*Abothrium rugosum*	Lühe	1910 : 26

Specific diagnosis: With the characters of the genus. Large cestodes with maximum length, breadth and thickness of 1000, 7 and 2mm., respectively. Scolex present only in very young strobilas, when conical and provided with very weak bothria, changing with age to a pseudoscolex of various shapes, usually imbedded in pyloric cecum of host. Proglottides at first broad and very short, obscured by irregular transverse and longitudinal rugae, then gradually lengthening with age until finally quadrate or longer than broad.

Cuticula 5μ thick, subcuticula 0.14mm. Small calcareous bodies, 20μ in length. Longitudinal muscles in bundles, transverse forming septa between proglottides. Nerve strands 45μ in diameter. Two chief excretory vessels anteriorly, passing into 30 to 35 posteriorly.

Genital cloaca irregularly alternating, between first and second thirds of edges of proglottides. Vagina opens immediately behind the cirrus and slightly ventral; no hermaphroditic duct.

Testes discontinuous from proglottis to proglottis, ellipsoidal, flattened anteroposteriorly, 40 by 90 by 85μ, and 45 to 60 in number. Vas deferens lateral to uterus-sac with few coils before entering the cirrus-sac, 350 by 70 to 80μ. Cirrus-sac ovoid with narrow end outward, 174 to 277μ long by 92 to 102μ in diameter. Cirrus straight in outer half of sac, proximally coiled or dilated.

Ovary large, entire, kidney-shaped (isthmus as thick as the wings), 0.6mm. wide, occupying the posterior half of the median portion of early mature segments. Ova conspicuous, nuclei large, 10 to 13μ in diameter. Oocapt 34μ in diameter. Beginning of oviduct S-shaped. Right and left vitelline ducts join ventrally; common duct acts as reservoir. Vitelline follicles entirely within longitudinal muscles, discontinuous, intermingling laterally with the testes, irregular in shape and size, largest 30, 90 and 70μ in length, width and thickness, respectively. Shell-gland compact. Uterine duct with only a few coils close to the median line; uterus-sac very wide and short, or irregularly circular or quadrate surficially, often lobed, 0.75 to 1.6mm. in transverse diameter, constantly rounded laterally; openings in median zig-zag row.

Eggs, 80 to 98μ long by 75 to 92μ wide, shell quite transparent.

Habitat: Intestine of the host with pseudoscolex imbedded in a pyloric coecum.

HOST	LOCALITY	COLLECTOR	AUTHORITY	
Gadus mustela	.....	Borke	Goeze	1782 : 410
Gadus mustela	.....	Wagler	Goeze	1782 : 411
Gadus aeglifinus	Warberg	Olsson	Olsson	1867 : 54
Gadus aeglifinus	Bergen	Lönnberg	Lönnberg	1890 : 22
Gadus aeglifinus	Grafverna and Näset	Olsson	Olsson	1893 : 17
Gadus aeglifinus	Arctic Ocean	Zool. Mus. d. K. Akad. Wiss., Petrograd	Linstow	1901 : 281
Gadus aeglifinus	England	Nicoll	Nicoll	1907 : 71
Gadus callarias	Woods Hole, Mass.	V. N. Edwards	Linton	1898 : 431
Gadus callarias	Arctic Ocean	Zool. Mus. d. K. Akad. Wiss., Petrograd	Linstow	1901 : 281
Gadus callarias	Murman-Küste	Zool. Mus. d. K. Akad. Wiss., Petrograd	Linstow	1903 : 19
Gadus callarias	Nokujev Id., Arctic	Zool. Mus. d. K. Akad. Wiss., Petrograd (Baer)	Linstow	1903 : 19
Gadus lota	Greiphswald	Rudolphi	Rudolphi	1810 : 43
Gadus merluccius	Rennes, France	Dujardin	Dujardin	1845 : 617
Gadus morrhua	Warberg	Olsson	Olsson	1867 : 54
Gadus morrhua	Grand Banks, Newfoundland	Lee	Linton	1890 : 750

HOST	LOCALITY	COLLECTOR	AUTHORITY
Gadus morrhua	Bergen	Lönnberg	Lönnberg 1890 : 23
Gadus pollachius	Rennes	Dujardin	Dujardin 1845 : 617
Gadus pollachius	Warberg	Olsson	Olsson 1867 : 54
Gadus pollachius	Bergen	Lönnberg	Lönnberg 1890 : 22
Gadus pollachius	Grafverna & Näset, Sweden	Olsson	Olsson 1893 : 17
Gadus pollachius	Millport, Scotland	Nicoll	Nicoll 1910 : 355
Lota vulgaris	.....	Siebold	Baird 1853 : 89
Lota vulgaris	Memel and Rossitten	Muehling	Muehling 1898 : 35
Lota vulgaris	Tvärminne Id., Finland	Schneider	Schneider 1903b : 8
Morrhua aeglifinus	England	Cobbold	Cobbold 1858 : 158
Morrhua vulgaris	England	Cobbold	Cobbold 1858 : 159
Morrhua vulgaris	Belgian coast	van Beneden	van Beneden 1871 : 56
Merlangus carbonarius	England	Cobbold	Cobbold 1858 : 159
Merluccius vulgaris	Warberg	Olsson	Olsson 1867 : 54
Melanogrammus aeglifinus	Woods Hole Region	.....	Sumner, Osborn and Cole 1913 : 586
Microgadus tomocod	Woods Hole Region	.....	Sumner, Osborn and Cole 1913 : 586
Urophycis tenuis	Woods Hole Region	.....	Sumner, Osborn and Cole 1913 : 586
Melanogrammus aeglifinus	Passamaquoddy Bay, New Bruns.	Cooper	Cooper (the present paper)
Melanogrammus aeglifinus	Bay of Fundy, Campobello Id.	Cooper	Cooper (the present paper)
Melanogrammus aeglifinus	Freeport, N. S.	Cooper	Cooper (the present paper)
Gadus callarias	Campobello Id.	Cooper	Cooper (the present paper)
Gadus callarias	Woods Hole Region	V. N. Edwards	Cooper (the present paper)

This species was first described by Goeze (1782:410) under the name of "Der runzlichter Fischbandwurm" and not as *Taenia rugosa*, as indicated by many later writers, including such authorities as Lühe, Braun and Ariola. It was Batsch (1786:208) who gave the specific name on the basis of Goeze's description. The latter, in fact, in a foot-note (p. 410) accepted Pallas' *T. tetragonoceps* to be synonymous with the forms he studied, at least in part, since he recognized that they were at the same time unlike those figured by Pallas after Bloch, from the "Madui-moräne" and the "Rheinlachs." It remained for Rudolphi (1810:42) to give a somewhat more detailed description, which seems to have been accepted by Diesing (1850, 1863) and others, altho Dujar-

din (1845:617) and Cobbold (1858:158) made important additions to the knowledge of the species. Van Beneden (1871:56) erected the new genus, which was later accepted by Lönnberg (1891:75) who used his specific name *gadi* as synonymous with the *B. rugosus* of the earlier writers. Fraipont (1880:267; 1881:12) added to the knowledge of the excretory system. It was not until some time later, however, that Linstow (1889:242) essayed to give a more detailed description of the whole worm, while Lönnberg (1891:75) and Matz (1892:113) by their attention to the anatomy, especially of the reproductive organs, laid the foundation upon which all the writers since have based their conceptions of the species. While the development, especially in its earliest stages, was studied by Schauinsland (1885:527), and later by Saint-Remy (1900:296), the systematic position has since then been dealt with by Blanchard (1894:701), Ariola (1896:272, 274; 1900:432), Riggenbach (1896:223) and Lühe (1899:33; 1900a:47, 96, 101; 1910: 26). Linton (1890:750; 1898:431) is the only writer who has described the species in America.

The dimensions of the species are, according to Lühe (1910:26), 400mm. to 1 meter in length by 2 to 5mm. in maximum breadth; while Ariola (1900: 433) gave the total length of the strobila as from 16 to 97cm. Linton (1890: 751) worked with specimens from the cod, the largest of which measured 655mm. in length by maximum breadth and thickness (posteriorly) of 6 and 2mm., respectively. The largest studied by the writer was a fairly contracted one (No. 301, below) from *Gadus callarias*, 416mm. in length by 7mm. in maximum breadth 100mm. from the incomplete posterior end and 5mm. at the posterior end.

As the names used by Goeze, Batsch and Rudolphi indicate, this species is characterized by its transverse wrinkles or folds, often irregular and complicated by longitudinal grooves and folds anteriorly but regular and corresponding to the internal segmentation posteriorly, and by the general tumid appearance of the strobila due to the very large uterus-sacs gorged with eggs. But most striking of all is the presence of a pseudoscolex which is found embedded in the intestinal coeca or intestinal wall of the host, from which it is extracted only by careful dissection. Goeze (1782:412, Figs. 1, 4 and 5) described a scolex, somewhat elongated, sagittate and irregular but otherwise comparable to that of other bothriocephalids, while Rudolphi (1810:43) does not seem to have found anything of such a structure in *Gadus lota*. Dujardin (1845: 617) was evidently the first to describe the pseudoscolex by saying that, " . . . la partie antérieure [of the strobila] engagée dans l'appendice pylorique forme une sort de bouchon, un cylindre irrégulier, cartilagineux, long de 18mm., large de 4mm., ride ou toruleux et sans ancune trace d'organisation . . . " This description, however, was not recognized by Diesing (1850:590), but he accepted Rudolphi's diagnosis, namely, "Caput subsagittatum, bothriis oblongis lateralibus. . . . " Baird (1853:89) evidently saw two bothria, probably owing to the fact that he was dealing with specimens from *Lota vulgaris* (vide infra). Cobbold (1858:158, 159) was well acquainted with the pseudoscolex, since regarding individuals from the cod ("*Morrhua vulgaris*")

he said "In a cod examined on the 15th of March, 1885, two specimens of *Bothriocephalus rogosus* had severally attained a length of nearly fifteen inches, and their anterior segments for an inch or more downwards, were so firmly impacted within the pancreatic coeca, that it was found impossible to dislodge them without injuring the filamentary head and neck. As if to make the anchorage doubly sure, the cartilaginous thickening of the invaded pancreatic coecum had degenerated into a calcareous and contracted cylinder, twisted upon itself in various ways." Olsson (1867:54) likewise found a pseudoscolex in this species, which he described as being degenerated in *Gadus morrhua* to a yellow, elongated mass which disintegrated on contact with water. It was 18 to 25mm. in length by about one-half a millimetre in diameter, while its position was, as usual, in the wall of a pyloric appendage of the host. He also figured a young strobila from *Gadus aeglifinus*, the scolex of which he considered to have been invaginated. In his new genus and species, *Abothrium gadi*, van Beneden (1871:56) observed the pseudoscolex stating that "Ils ont la tête vers le fond des coecums pyloriques, percent ordinairement les parois et forment, par la gaîne, souvent dure et entortillée comme une tabulaire, une saillie à la surface de cet organe." So far as the writer is aware, he gave the first figure of the structure, as it is commonly met with, encased, however, by the walls of the pyloric coecum in which it was found lodged. Von Linstow (1889:242) described and figured a scolex somewhat similar to that of *A. crassum*, excepting that the apex was hollowed out to form a six-cornered opening which communicated with both bothria. Linton (1890: 750) found pseudoscolices in examples from the codfish, "*Gadus morrhua*," which were much as described by Olsson, since he said that "each of the specimens in this lot has the head and anterior part of the body buried in the pyloric caeca, where they have undergone degeneration to such an extent that no appearance of bothria remains. Around the parts thus enveloped by the caeca is a yellowish waxy deposit, the degenerated tissue of the caeca. This adventitious tissue invested the worm so closely that it would be absolutely impossible for the parasite to free itself from its host." The next important reference to the scolex was by Lönnberg (1891:75) who, while accepting van Beneden's new genus, *Abothrium*, referred the species back to *rugosum* of Batsch, and described the metamorphosis of the anterior end of the strobila into the well-known pseudoscolex, accounting for the various forms, such as figured here. It is noteworthy, however, that he did not state specifically that bothria are present in very young scolices, before this transformation takes place, nor did he give any figures to illustrate the latter. Matz (1892: 114) described and figured a typical scolex for a specimen 36cm. long from *Lota vulgaris*, while Schneider (1903a:9) in delineating a similar structure for the species from the same host, pointed out its great similarity to the scolex of *B. proboscideus* (=*A. crassum*). Perhaps of significance in connection with the question of the metamorphosis of the organ is his statement that "Der ganze Scolex kann sich nämlich durch verschiedene Contraction seiner Muskeln in ein pfeilförmiges, oder fast cubisches, oder sogar sichelförmiges Gebilde

verwandeln." Later Johnstone (1907:170) described the pseudoscolex with considerable detail, finding quite the same conditions as did Linton. On account of never meeting with anything like a typical scolex in adult worms he was led to conclude that "Probably in young codling, recently infected, a stage of the cestode with such a scolex might be found but doubtless with increasing age the changes mentioned above occur, and the normal structure of the head disappears." And lastly, Scott (1909:85) made somewhat similar statements, pointing out that " . . . no satisfactory description of this part of the worm [the pseudoscolex] has yet been published." Thus it is seen that, apart from Olsson's (1867:54) finding in *Gadus aeglifinus* of a possible young stage in the degeneration of the scolex of this species, no one has, as yet, figured in detail its metamorphosis, Lönnberg, however, giving the only description of the process. On the other hand, a typical scolex has been described by several writers, as pointed out above, for what has been taken to be the same species in *Lota vulgaris*, but since there is evidence that the latter is quite different from the species found in marine Gadidae and since the specimens from *Lota maculosa*, studied by the writer, were found to belong to the well known *A. crassum*, a pseudoscolex must be attributed only to adults of *A. rugosum*, at least until the confusion which exists in the literature regarding the form from Lota can be cleared up by further investigation.

Two forms of pseudoscolex which were dissected out by the writer from the pyloric ceca of *Melanogrammus aeglifinus*, the haddock, and *Gadus callarias*, the cod, are shown in figures 35, 36, respectively, the latter being from the largest specimen at hand; while what is doubtless a younger stage in the degeneration of the scolex is shown in figure 34 from the intestine of a haddock. A series of transverse sections of the latter, brought out that the internal anatomy was quite suggestive of a typical scolex, that of *A. crassum*, for example. As shown in the figure, the structure is somewhat flattened in the dorsoventral direction. While there were only faint suggestions of bothria, especially towards the tip, the arrangements of the muscles, nerves and excretory vessels pointed to its being possibly not far removed from the typical form of scolex. This view is supported by the fact that it was found free in the anterior part of the intestine of the haddock, altho, unfortunately, the length of the strobila was not recorded. Among a lot of material taken from several haddock two examples of the true scolex, as it would seem to be at or about the time degeneration sets in, were found. The first one, shown in figure 32, was from the smallest strobila at hand, 22mm. in length, while the other, figure 33, was from an older chain, only the anterior end of which was present with a length of 32mm. and maximum breadth of 2.5. The second is evidently the older from the standpoint of metamorphosis, since it is more conical and less separated from the neck region which is slightly swollen; while the bothria are disappearing as the whole structure is approaching the stage represented by figure 34. In figure 32 are seen somewhat more efficient bothria, but the shape of the organ points to a considerable amount of degeneration having already taken place. The next stage in the degeneration of the scolex

is represented by figure 35. Here the structure is likewise not embedded in the wall of the pyloric cecum in which it is found but free in its lumen, the anchorage for the strobila being obtained by the close approximation of the mouth of the cecum around the narrow neck region and the concomitant swelling of the more distal portions. Furthermore, the indications are that a considerable portion of the anterior end of the strobila is involved in the formation of the organ, especially since it is comparatively large. The final stage is that shown in figure 36, where degeneration has gone on to such an extent that there remains only a filamentous, horny or cartilaginous yellow mass, deeply and firmly embedded in the wall of the cecum. Only the tip is shown, there having been about 6mm. more to the region where it left the host tissues and passed insensibly on to the anterior portion proper of the strobila. The latter showed only faint transverse wrinkles and no distinct division into segments, as is seen, with some irregularity, however, in figure 32. This form of pseudoscolex was found, as described by Olsson, Linton and Johnstone, to be surrounded by the tissue of the cecum degenerated to a yellow waxy mass which, when freed from the surrounding tough tissue, crumbled easily under the dissecting instruments.

The strobila, at first almost cylindrical in shape, gradually becomes wider and more depressed until the maximum breadth near the posterior end is attained. As regards the form of the segments Dujardin said that, ". . . le reste du corps long de 100 à 140mm., large de 2mm. en avant et de 6.5 en arrière, est libre dans l'intestin et formé d'articles tres courts, inégaux ou dilatés ca et là; . . ."; and Linton stated that, "The body is not distinctly segmented at first, but is crossed by innumerable fine wrinkles." While the latter statement is in the main true, and applies particularly to the youngest strobilas, many species show that these rugae, altho much obscured by irregular longitudinal grooves, are simply due to the formation of extremely short segments which correspond proportionately with the much more distinct ones farther back. These segments gradually elongate as they pass backward until the end proglottides are often quadrate or even longer than broad, depending on the degree of contraction or relaxation. Linton gave the length of the segments near the middle of the strobila as from 0.7 to 1.0mm. and posteriorly 0.45, and the thickness as 2mm. The latter was 2.5mm. in the largest specimen examined by the writer. The openings of the uteri on the ventral surface of the strobila form collectively a sort of shallow groove, more pronounced, of course, posteriorly but quite obliterated when the segments are considerably relaxed.

The anatomy of the species was first given careful attention by Linstow (1889:235). Later Lönnberg (1891:75) and Matz (1892:113) published more accurate descriptions to which most of the writers since have referred. That of Lönnberg was found, however, to be most applicable to the material at hand from the cod and the pollack, for Matz was dealing with specimens from *Lota vulgaris* and Linstow apparently confused the two possible species from Lota and the marine Gadidae (*vide infra*).

Linstow included in his conception of the cuticula not only the cuticula proper, which he stated was 3.3μ in thickness, but also the outer clear zone of the subcuticula which he found to be 49μ thick. In the present study the cuticula was found to be about 5μ thick and to be divided into the three zones described by Lönnberg; viz., an outer pseudociliated or ragged layer, occupying almost one-half of the thickness of the whole membrane, a middle homogeneous principal stratum, and an innermost basement membrane which stands out quite distinctly in this species without the use of any special stains. The subcuticula was found to average 0.14mm. in thickness, the clear outer ends of the elongated cylindrical and closely crowded cells being collectively 23μ thick. The whole cortex in transverse sections has a depth of 0.32mm. Small calcareous bodies, quite difficult to distinguish from parenchymatous nuclei, are present as described and figured by Lönnberg. They are oval to elliptical in outline and have a maximum length of 20μ.

The musculature is well developed, and is peculiar in that the sagittal fibres especially retain their myoblasts, which are very easily recognized in sections. "They extend from the dorsal to the ventral surface and are usually attached to the cuticula with their ends, but often fasten on to the walls of the excretory vessels or other organs. Their number rises considerably with increasing age of the proglottis. Since they pass thru the spaces between the bundles of longitudinal muscles, they are partially arranged in fasicles. These muscles have not only a nucleus, but often also surrounding the same a quite large, spindle-shaped protoplasmic mass; and one easily finds the different developmental stages from a spindle-shaped cell to fully developed muscle fibres of typical appearance, where the protoplasm is already transformed and reduced, and only the nucleus persists." They are only slightly more numerous between the sets of reproductive organs than elsewhere. In this region, on the other hand, the transverse series form, as emphasized by Lönnberg, a distinct partition separating all constituents of the genitalia of successive proglottides,the testes and vitelline follicles especially (cf. *A. crassum*). In transverse sections they form a "plate," bounding the medulla externally on each surface, from which a few fibres pass farther out among the bundles of longitudinal muscles. The latter are arranged in two distinct layers, each about 0.15mm. in thickness in the median line, which gradually diminish towards the edges of the strobila where they join thru several small and very irregular bundles. These larger fasicles are further subdivided dorsoventrally into smaller ones of various sizes, all of which are connected longitudinally, however, by strands passing from one to the other, as pointed out by Lönnberg. In the anterior end of the strobila, as one follows them forwards, the fasicles of longitudinal fibres become less and less distinct, but extend to the tip of the scolex, or young pseudoscolex, as the case may be, scattering considerably as they go. In sections thru the structure shown in figure 33, a small number of sagittal and transverse fibres and a very few radial ones, situated between the grooves seen externally proves that it is a scolex, but a poorly developed one, or, as indicated above, one showing early stages in the process of degeneration to form the

pseudoscolex. This latter statement applies in a greater degree to the structure shown in figure 34, since in it still more degeneration is present to the extent that no traces of the radial fibres are to be seen altho there are very shallow bothrial depressions. In each case there appears in the medulla and among the longitudinal muscles near the tip of the organ a considerable amount of a material which takes the Orange-G counterstain very readily. While this is relatively more abundant in the older of the two pseudoscolices in question and intermingled with a good deal of calcareous material, it is confined more to the very tip of the younger organ. It represents possibly the first stages in the development of the yellow horny material seen in the oldest and most degenerate pseudoscolices.

Each of the chief nerve strands has a diameter of about 45μ and is situated usually dorsal to the cirrus and vagina, but occasionally ventral. Linstow (1889:243) gave the diameter as 56μ. Near the scolex of the youngest strobila at hand it was found to be only about 34μ and traversed with transverse and sagittal muscle fibres. Within the scolex the two strands gradually converge and become united between the bothria by several weak and indistinct strands in lieu of a commissure.

The excretory vessels are small and irregular in number and arrangement in the mature segments. Lönnberg gave their number as 10 in young segments and from 30 to 35 in mature proglottides, but anteriorly and in young strobilas, there are two chief canals, as stated by Linstow, close within the nerve strands, accompanied by several smaller ones. They break up in the pseudoscolex into an irregular plexus and posteriorly in the youngest strobilas empty into the terminal vesicle, shown in figure 63.

The first traces of the rudiments of the reproductive organs were seen 5.2mm. from the anterior end of the smallest strobila found, which was 22mm. in length. The genital cloacae alternate irregularly from side to side, altho they may be situated on one side for stretches involving at least five proglottides. Dujardin (1845:617) described them as being unilateral or very irregularly alternating, while Linstow (1889:244) said they were one-sided, and between the middle and hinder one-third of the edges of the proglottides. In the sections made they were found between the first and second thirds, often covered by the edge of the proglottis next ahead and from 35 to 75μ in depth. Since the actual opening is usually closed by the longitudinal contraction of the strobila, it is difficult to distinguish it externally from grooves separating consecutive proglottides or other lateral grooves between irregular rugae. The vagina opens immediately behind the cirrus and slightly ventral, there being no distinct ductus hermaphroditicus. This corresponds with Lönnberg's and Linton's finds, whereas Linstow said that it is opened ahead of the cirrus.

The testes are arranged in two lateral fields between the nerve strands and the uterus and ovary in the median line, and are strictly discontinuous, that is, separated longitudinally into sets corresponding with the other genitalia by the transverse muscular septa between proglottides. Their average maximum length, width and depth are, respectively, 40, 90 and 85μ, thus indicating

that they are usually quite flattened anteroposteriorly. Linstow gave the diameter as 0.06mm. As stated by Lönnberg, they show various stages in the development of spermatozoa quite well. Altho Linstow described them as being arranged in an elongated half-ring on each side, they were found by the writer to occupy all parts of the medulla in the fields indicated, intermingling irregularly with the vitelline follicles, but in general more numerous in the median frontal plane. From 23 to 30 are present in each lateral field, thus making the total number for the proglottis from about 45 to 60. The vas deferens forms an elongated mass of coils in the anterior portion of the proglottis, which extends from the uterus-sac to the cirrus-sac, near which its coils are fewer in number and more openly arranged. The whole mass has a length (transversely) of 0.35mm. by a diameter (longitudinally) of 0.07 to 0.08. As pointed out by Lühe (1900a) the duct forms within the cirrus-sac a proximal winding ductus ejaculatorius—it is often quite dilated—and a distal straight cirrus proper, which occupies half the length of the sac. The cirrus-sac varies in length from 174 to 277μ and in maximum diameter, medially, since the whole is ovoid with the narrow end outward, from 92 to 102μ. Lühe gave the measurements as 220 by 75 to 90μ. As noted by the same writer, myoblastic nuclei form such a thick layer outside of the wall and there are so many parenchymatous nuclei within the sac, that the wall itself is at first difficult to locate in sections. The cirrus proper may have a dorsoventral diameter of 40μ.

The vagina has a diameter of 20μ as it passes the cirrus-sac, and is lined with a comparatively thick cuticula. Lühe stated that the ventral bow in its course is more median than in *A. crassum*, but in the material sectioned the very reverse was found to be the case. The ovary of this species is very conspicuous since it is large (0.6mm.) wide compact and somewhat kidney-shaped; Linstow's measurements are 0.14mm. wide by 0.12 long. There is no distinct isthmus, or, as Lönnberg stated, there is a very broad one, both longitudinally and dorsoventrally, from the middle of the anterior face of which the oviduct arises either towards the dorsal or the ventral surface. The ova are large and conspicuous because of their prominent nuclei which are from 10 to 13μ in diameter, while their nucleoli are about 2.5μ. Linton (1890: 752) gave these data as 8 to 14 and 2.5μ, respectively. The oocapt has a diameter of about 34μ. From it the oviduct proceeds laterally at first, then with a sharp turn back, i.e., "towards the side opposite the genital-opening," it is joined by the vagina just before it makes a second turn towards the dorsal surface of the proglottis (Fig. 109). The viteline follicles are, as stated by Lönnberg, entirely within the parenchymatous muscle-sac—and thus discontinuous longitudinally—altho Lühe (1910:26), probably basing his statements on Matz's (1892:113) description, said that they are ". . . zum Teil noch nach inner von der Längsmuskulatur." They are arranged in two lateral fields corresponding to those occupied by the testes with which they intermingle freely, altho being situated more peripherally. They are somewhat irregular in shape and size, but usually compressed anterposteriorly, and as much as 90μ wide, 30 long and 70 thick. There is a median field free of them

both dorsally and ventrally. Right and left vitelline ducts passing to the median line close to the ventral layer of transverse muscles unite ventrally to form a common duct, which acts as a yolk reservoir. The union of the common vitelline (Fig. 109) duct with the oviduct takes place in the median frontal plane, a little aside from the median line and just beyond the bend in the oviduct before which is located the point of union of the vagina. The shell-gland is quite compact and situated close to the dorsal wall of the medulla. The uterine duct takes only a very few short coils, mostly in the dorsoventral direction close to the median line, before passing into the very capacious uterus-sac. The latter vies with the large ovary in filling up the median portion of the medulla, and measures in mature (not gravid) proglottides, 0.74mm. wide, 0.74 long and 0.37 deep, being obviously quite flattened in the antero-posterior direction as are the other organs. In mature proglottides which are quadrate in shape it may be still somewhat elliptical in outline, as much as 1.6mm. long by 1.3mm. wide, and show distinct lobations; whereas the widest and most gravid joints may be little else than sacs of eggs, the rest of the reproductive system in both cases having almost entirely degenerated. The uterus-sacs were constantly found to be rounded or lobate laterally, as stated by Matz and Lühe. The openings form a somewhat irregular zig-zag row on the ventral surface of the strobila, without, however, being accommodated in a distinct groove.

The eggs, taken from gravid uteri and measured in the formalin in which the strobilas were preserved, were, externally, 80 to 98μ long by 75 to 92 wide; mantle, 67 by 62μ; "ectoderm" (of Schauinsland), 62 by 54μ; and oncosphere, 52 by 40μ. The similar data given by Dujardin, which were considered by Linstow to be not of this species, were: shell, 80 to 110 by 50 to 57μ; "ectoderm," or inner shell, 51 to 57μ; oncosphere, 48 to 50μ. Linstow's figures, copied by Lühe, were 59 by 43μ.

The earliest stages in the development of this species have long been known from the work of Schauninsland (1885:527), who followed it to the escape of the oncosphere enclosed in the non-ciliated mantle. Saint Remy (1900:296-7) thought that he probably saw polar bodies and the male and female pronuclei among other important finds, and came to the conclusion ". . . que les phénomènes sont essentiellement les mêmes chez les Bothriocéphales et chez les Taenia et se résument dans la constitution de deux enveloppes autour de l'embryon hexacanthe." Olsson found a small strobila 22mm. in length in *Gadus aeglifinus*, which he considered to belong to this species; but apart from this there seem to be no other references in the literature to the development of the strobila from the plerocercoid. As stated above, the smallest found by the writer was also 22mm. in length, but no such invagination of the scolex as mentioned by Olsson was observed.

As stated above, there is considerable evidence in the literature of this species to indicate that the form found in marine Gadidae and called *A. gadi* by van Beneden (1871:56) is not the same as that found in the only fresh-water gadid, viz., Lota. In endeavoring to place a number of specimens from *Lota maculosa*, it was found that in many points they agreed with the descrip-

tion given by Matz for *A. rugosum*. The scolices are more or less alike, no pseudoscolex (see below, however) being present; the longitudinal muscles are not in bundles; the genital cloacae are irregularly alternating from side to side; the vagina opens ahead of the cirrus instead of behind; the testes are continuous from proglottis to proglottis; the vitelline follicles are located among the longitudinal muscles and are discontinuous; and the uterus-sacs are rounded laterally. In most of these and in many more points, on the other hand, the form agrees with *A. crassum*, so that the writer is obliged to consider it to belong to that species. Furthermore, a direct comparison of Matz's description with that of Lönnberg brings out many differences. Lönnberg described a pseudoscolex, calcareous bodies, the longitudinal muscles in bundles, the other sets of parenchymatous muscles as above described, the vagina opening behind the cirrus and ventrally, testes discontinuous, vitelline follicles within the parenchymatous muscle-sac and also discontinuous, none of which characters are to be found in Matz's description, but all of which apply to the material at hand from marine Gadidae. It is to be noted here that Lönnberg accepted the specific name *rugosum* of Rudolphi instead of the *gadi* of van Beneden, which as will be seen presently may not be admissable. Going back, then, to the only other and the earliest description of the anatomy of the species, namely, that of Linstow (1889:242-5), similar difficulties and confusion are met with. Linstow gave as hosts for the species, which he called *B. rugosus* Rud., *Gadus aeglifinus*, *G. morrua*, *Merlangus carbonarius*, *M. pollachius*, *Merlucius vulgaris*, *Lota vulgaris*, *L. molva* and *Motella mustela*. Characters in his description not applicable to the material studied are: No pseudoscolex, but scolex of a rather peculiar shape and structure terminally; nerve strand 56μ in diameter; 10 excretory vessels anteriorly arranged in two groups of five each; genital cloacae unilateral, between the middle and hinder thirds of the edge of the proglottis; vagina opening ahead of the cirrus; length of cirrus-sac 0.42mm. (!); ovary 0.14 by 0.12mm.; uterus spherical when obviously young; and eggs 59 to 43μ. Testes with a diameter of 60μ, vagina 16 to 26μ in diameter at the beginning, and two vitelline ducts, besides a few other minor points in the general anatomy, agree, however, with the species as studied by the writer. Thus it is seen there is by no means anything like complete agreement as regards details among the three descriptions by Linstow, Lönnberg and Matz. But this does not seem to have inconvenienced many of the writers since then, notably Ariola (1900:432) and even Lühe (1900a) whose references to the position of the vitelline follicles and the ventral bow in the vagina are at variance with conditions described here; altho Johnstone (1907), Scott (1909) and Nicoll (1910) were obviously dealing with the form described by Lönnberg, Schneider (1903a:7-10) seems to have been the only one who pointed out the differences between the form from Lota and that from marine Gadidae. He said: "*Bothriotaenia rugosa* gleicht sowohl in ihrem Aussehen, als auch in ihrer Anheftungsweise ausserordentlich der Species *B. proboscidea*, die in unseren Lachsen (*Salmo salar*) so massenhaft vorkommt. Trotzdem pflegt man aber seit Rudolphi, soviel mir bekannt, immer die in Lota meist vorkom-

mende Form als eine getrennte Species auf zufassen unter dem Namem '*rugosa*' (*Bothriocephalus rugosus* Rud. = *Dibothrium rugosum* Diesing, u.s.w.), obgleich die unterscheidenden Merkmale zwischen *B. proboscidea* und *B. rugosa*, die Riggenbach in seinen 'Bemerkungen ueber das Genus *Bothriotaenia* Railliet' übersichtlich zusammenstellt, recht unbedeutend sind und vielleicht doch noch in Rahmen der Variationsbreite einer einzigen Species untergebracht werden können;" and, as regards the latter, in a footnote: "Die von M. Lühe . . . als Unterscheidungsmerkmal vorgeschlagene Lage der Dotterstöcke zum Theil (*B. rugosa*), bzw. auschliesslich (*B. proboscidea*) zwischen den Längsmuskeln, scheint mir auch nicht genugend constant sein, um als Speciesmerkmal verwandt werden zu können." For material from *Lota vulgaris* Schneider described a scolex and segments both similar, as he pointed out, to those of *B. proboscidea* (= *A. crassum*). The arrangement of the genital cloacae, irregularly alternating but unilateral for long stretches, the openings of the uteri in a longitudinal furrow, the early form of the uterus-sac and the size of the eggs (64.5 by 50 to 52μ), as described by the same worker, all agree with *A. crassum* as studied by the writer. In conclusion Schneider said: "Uebrigens habe ich, wie gesagt, auch an die Examplaren aus dem Museum keine Pseudoscolexbildung bemerkt und zweifle daran, dass *B. rugosa* und *B. gadi* ein und dieselbe Art sind," and further, "Es ist mir übrigens bisher noch nicht gelungen, *B. rugosa* oder *B. gadi* in *Gadus morrhua* des Finnischen Meerbusens aufzufinden, obgleich ich zahlreiche Exemplare des Dorsches seciert habe, und obgleich *B. rugosa* in *Lota vulgaris* hier oft genug vorkommt. Auch das scheint gegen die Identität der Species *B. rugosa* mit *B. gadi* zu sprechen."

Thus it is seen that there is considerable detailed evidence that the species from Lota is not the same as that from the marine hosts. One must then go back of Linstow's time in order to determine, if possible, what is the correct name for the latter. Next in retrogressive order is van Beneden's (1871:56) description of *A. gadi*, confined to a short footnote which deals with little more than the pseudoscolex. So far as it goes this agrees with Lönnberg's *A. rugosum* and with the material studied by the writer. Olsson (1867:54) was obviously dealing with the same form which he reported from marine hosts only. Diesing (1863 and 1850) copied from Rudolphi, while Cobbold (1858) had the marine form before him, and Baird (1853) had the fresh-water form. In spite of Linstow's objection the writer feels certain that Dujardin (1845) also had the species dealt with here, especially since his measurements of the eggs come nearest to those observed than do those of any other writer. It remains then to enquire into Rudolphi's finding and description, as Leuckart (1819:57) copied from him altho at the same time remarking that "Ist am nächsten mit den *B. proboscideus* verwandt, und, wenn er nicht eine Art mit diesem ausmacht zwischen *B. proboscideus* und *B. sagittatus* zustellen." For *B. rugosus* Rudolphi (1810:42) described a scolex, comparable to that of his *B. proboscideus* and to Linstow's description and figure of the organ, no neck, and segments "primi angusti, fere quadrati, insequentes latitudinis ratione habita brevissimi, saepeque inequales, vel hinc inde angustiores; margines obtusi crassiusculi."

This, with "neque ovaria, neque foramina articulorum vidi . . . " and the further fact that he obtained his specimens from *Gadus lota* (=*Lota vulgaris*), leads the writer to believe that he was not dealing with the form present in marine hosts but with a form which, if not identical with *A. crassum* (=his *B. infundibuliformis* and *B. proboscideus*), was very close to it. One must then go back farther to Batsch (1786:208) where the species *T. rugosa* was named on the basis of Goeze's (1782:410) description of "Der runzlichter Fischbandwurm" from *Gadus mustela* (=*Motella mustela*), the marine five-breared rockling of Europe, which the latter called *T. tetragonoceps* Pallas, with some doubts, however, as discussed under the next species dealt with here. Batsch gave the following diagnosis of *T. rugosa:*

"Taenia (larvata) capite conico cum corpore subconfluente, papillis lateraliter adnatis usque ad apicem capitis, eisque binis: articulis brevissimis, dilatatis, corpore serrato."

He used Goeze's figures 1 to 4 and pointed out that he (Goeze) recognized differences between his specimens and Pallas' *T. tetragonoceps*, for "Er rechnet beyde Würmer fur eine Art, und die Glieder nebst dem ganzen Korper haben viel Gleichheit, auch die äussere Gestalt des Kopfs. Doch sind bey diesem letztern die Saugblasen bey weiten nicht so deutlich gezeichnet, und stellen vielmehr, wie sich Götze ausdrückt, zwey Backenbarte vor. Die Furche auf dem Korper ist auch vorhanden, nur scheint der Korper mehr gestreckt, und am Rande mehr zackig zu seyn." Consequently the correct name of the species depends on whether Goeze's description, augmented by Batsch's contributions, is considered to be applicable to the material at hand. The largest of Goeze's specimens measured in warm water a yard and half in length by scarcely one-half a line in breadth; but the latter is decidedly at variance with his figures 1 and 2 which he said were drawn in "natürlicher Grösse," in which case the width would be from 7 to 15 lines and the scolex about 17.5 lines in length! For these large specimens—even tho only the first set of measurements were taken into consideration—he described and figured nothing of diagnostic value other than a scolex provided with two bothria pretty much of the ordinary type, behind this a "distinctly jointed" and "almost cylindrical" neck and along both surfaces of the posterior closely crowded segments a median longitudinal furrow, all of which characters more nearly agree with the *proboscideus* type of *A. crassum* rather than with the *A. rugosum* described here. And since the latter is clearly not *T. tetragonoceps* Pallas as described by Batsch (1786:204), the only course that seems open is to refer the species to van Benden's *Abothrium gadi.* However, in view of the fact that no material from the European ling (*Lota vulgaris*) was available for a comparative study, the writer does not feel justified in taking this step, but here retains at least tentatively the specific name *Abothrium rugosum* (Batsch 1786), nec *A. rugosum* Goeze 1782.

The material studied consisted of lots 295, 296, 297, 298, 299, 300, and 302 from *Melanogrammus aeglifinus* (L.), the haddock, and 301 from *Gadus callarias*, the cod in the writer's collection; and 17.53 in the collection of the University of Illinois, also from the cod.

ABOTHRIUM CRASSUM (Bloch 1779)

[Figs. 37-42, 50-54, 64, 77, 92]

1779	*Taenia crassa*	Bloch	1779 : 545
1780	*Taenia salmonis*	Müller	1780 : 179, 202
1781	*Taenia tetragonoceps* (part.)	Pallas	1781 : 87
1782	*Taenia capite truncato*	Bloch	1782 : 410
1782	"Der runzlichter Fischbandwurm"	Goeze	1782 : 410
1782	*Taenia proboscis suilla*	Goeze	1782 : 417
1786	*Taenia tetragonoceps*	Batsch	1786 : 204
1786	*Taenia proboscidea*	Batsch	1786 : 212
1790	*Taenia salmonis*	Gmelin	1790 : 3080
1790	*Taenia salvelini*	Schrank	1790 : 125
1793	*Taenia salvelini*	Schrank	1793 : 141
1795	*Taenia salmonis*	Rudolphi	1795 : 17
1802	*Taenia salmonis*	Bosc	1802 : 308
1802	*Taenia proboscidea*	Rudolphi	1802 : 106
1803	*Rhytis salvelini*	Zeder	1803 : 292
1810	*Bothriocephalus proboscideus*	Rudolphi	1810 : 39
1810	*Bothriocephalus infundibuliformis*	Rudolphi	1810 : 46
1816	*Bothriocephalus proboscideus*	Lamarck	1816 : 582
1819	*Bothriocephalus proboscideus*	Rudolphi	1819 : 137, 472
1819	*Bothriocephalus infundibuliformis*	Rudolphi	1819 : 137, 473
1819	*Bothriocephalus proboscideus*	Leuckart	1819 : 38
1819	*Bothriocephalus infundibuliformis*	Leuckart	1819 : 42
1843	*Bothriocephalus salmonis umblae*	Koelliker	1843 : 91
1844	*Bothriocephalus proboscideus*	Bellingham	1844 : 252
1844	*Bothriocephalus infundibuliformis*	Bellingham	1844 : 253
1845	*Bothriocephalus proboscideus*	Dujardin	1845 : 615
1845	*Bothriocephalus infundibuliformis*	Dujardin	1845 : 616
1846	"Bothriocephalus du Saumon"	Blanchard	1847 : 116
1850	*Dibothrium proboscideum*	Diesing	1850 : 590
1850	*Dibothrium infundibuliforme*	Diesing	1850 : 590
1853	*Bothriocephalus proboscideus*	Baird	1853 : 88
1853	*Bothriocephalus infundibuliformis*	Baird	1853 : 88
1863	*Dibothrium proboscideum*	Diesing	1863 : 242
1863	*Dibothrium infundibuliforme*	Diesing	1863 : 242
1867	*Bothriocephalus proboscideus*	Olsson	1867 : 53
1871	*Bothriocephalus proboscidea*	van Beneden	1871 : 69
1878	*Bothriocephalus infundibuliformis*	Linstow	1878 : 263
1884	*Bothriocephalus infundibuliformis*	Zschokke	1884 : 21
1889	*Bothriocephalus suecicus*	Lönnberg	1889 : 35
1892	*Bothriocephalus infundibuliformis*	Matz	1892 : 110
1893	*Bothriocephalus infundibuliformis*	Olsson	1893 : 17
1893	*Bothriocephalus proboscideus*	Olsson	1893 : 17
1894	*Bothriotaenia infundibuliformis*	Blanchard	1894 : 701
1896	*Bothriotaenia infundibuliformis*	Ariola	1896 : 280
1896	*Bothriotaenia infundibuliformis*	Riggenbach	1896 : 223
1899	*Abothrium crassum*	Lühe	1899 : 39
1900	*Bothriotaenia proboscidea*	Ariola	1900 : 433
1900	*Abothrium crassum*	Lühe	1900a : 97
1909	*Bothriocephalus proboscideus*	Scott	1909 : 78
1910	*Abothrium crassum*	Lühe	1910 : 26
1910	*Abothrium crassum*	Ward	1910 : 1184

Specific diagnosis: With the characters of the genus. Large cestodes with maximum length, breadth and thickness of 870, 6 and 2mm., respectively. Scolex variously shaped; usually rounded posteriorly and truncated anteriorly; with prominent bothria and terminal disc. First segment may or may not be elongated to form a short neck. Proglottides at first broad and short or more quadrate, cuneate or infundibuliform in shape; in the middle of the strobila, five or more times broader than long; posteriorly, quadrate or as long as broad. Usually a median longitudinal groove down each surface of the strobila formed by emarginations on the posterior borders of the segments.

Cuticula 4 to 6μ thick, subcuticula 40 to 100μ. Calcareous bodies (?) absent in adult strobilas. Longitudinal muscles not in bundles; no muscular septa between proglottides. Nerve strands 25 to 40μ in diameter, dorsal to inner end of cirrus-sac. 12 chief excretory vessels, 6 on each surface just within the transverse muscles, reduced to 6 or 8 anteriorly.

Genital cloaca irregularly alternating, but unilateral for long stretches; from one-third to one-half way along the margin of the proglottis. Vagina opens ahead of and slightly ventral to the cirrus; no distinct hermaphroditic duct.

Testes within the nerve strands, pseudostratified, continuous from joint to joint; elongated dorsoventrally, 95 to 115 by 70 to 100μ; 40 to 150 in number. Vas deferens lateral, elongated, with few coils before entering the cirrus-sac, 350 to 600 by 100 to 180μ in dimensions. Cirrus-sac ovoid with narrow end outward, 130 to 380 by 60 to 150μ. Cirrus proper an almost straight tube in outer half of sac.

Ovary comparatively small, irregular or somewhat lobed, with thick isthmus, 0.8mm. wide by 0.13 long. Oocapt 40μ in diameter. Usually two ventral vitelline ducts unite to form a common duct which does not act as a reservoir. Vitelline follicles irregular in shape and size, among the longitudinal muscles or outside of them, discontinuous. Shell-gland small, compact, dorsal. Uterine duct with only a few coils near the median line. Uterus-sac transversely elliptical or somewhat quadrate and slightly lobed, rounded laterally filling up almost the entire proglottis when gravid; opening in the median line opposite emarginations of segments ahead.

Eggs, 45 to 115 by 30 to 75μ; ovoid or ellipsoid in shape.

Habitat: In the pyloric coeca and intestine of the host.

HOST	LOCALITY	COLLECTOR	AUTHORITY
Salmo salar	.....	Borke	Goeze 1782 : 417
Salmo salar	Gryphswald	Rudolphi	Rudolphi 1819 : 137
Salmo salar	Ireland	Bellingham	Bellingham 1844 : 253
Salmo salar	Paris	Dujardin	Dujardin 1845 : 615
Salmo salar	.....	M. C. V.	Diesing 1850 : 590
Salmo salar	.....	Siebold & Johnston (Coll. Brit. Mus.)	Baird 1853 : 88

HOST	LOCALITY	COLLECTOR	AUTHORITY
Salmo salar	Warberg	Olsson	Olsson 1867 : 53
Salmo salar	Belgian coast	van Beneden	van Beneden 1871 : 69
Salmo salar	Warnemünde	Zschokke	Braun 1891 : 55
Salmo salar	Näset	Olsson	Olsson 1893 : 17
Salmo salar	Rhine R., Basel	Zschokke	Zschokke 1896 : 776
Salmo salar nobilis	Murman-Küste	Zool. Mus., Kais. Akad. Wiss., Petrograd	Linstow 1903 : 20
Salmo salar sebago	Lake Sebago, Me.	Ward	Ward 1910 : 1184
Salmo alpinus	.....	Mus. Vienn.	Rudolphi 1819 : 137
Salmo alpinus	Jenitland	Olsson	Olsson 1876 : 149
Salmo alpinus	Lakes Nackten, Störsjön, Locknesjön	Olsson	Olsson 1893 : 17
Salmo carpio	L. Garda, Italy	Ninni	Stossich 1890 : 7
Salmo caspius	Karabugas-Strasse	Maximovic	Linstow 1903 : 20
Salmo fario	Ireland	Bellingham	Bellingham 1844 : 252
Salmo fario	Rome	Condorelli	Ariola 1900 : 435
Salmo fario	Vyg-Fluss	Danilevskij	Linstow 1903 : 20
Salmo hucho	.....	Mus. Vienn. and Bremser	Rudolphi 1819 : 472
Salmo lacustris	Benaco	Largaiolli	Ariola 1900 : 435
Salmo namaycush	Shoal Id., Lake Superior	Milner	Ariola 1900 : 435
Salmo salvelinus	.....	Schrank	Stiles & Hassall 1912 : 402
Salmo salvelinus	.....	Zeder	Stiles & Hassall 1912 : 403
Salmo salvelinus	.....	Mus. Vienn.	Rudolphi 1819 : 137
Salmo salvelinus	.....	Diesing	Diesing 1850 : 591
Salmo siscowet	Outer Id., Lake Superior	Milner	Ariola 1900 : 435
? *Salmo thymallus*	.....	Coll. Vienn.	Leuckart 1819 : 43
Salmo thymallus vexillifer	.....	M. C. V.	Diesing 1850 : 591
Salmo trutta	Ireland	Bellingham	Bellingham 1844 : 253
Salmo trutta	.....	Coll. Brit. Mus.	Baird 1853 : 88
Salmo trutta	Lakes Störsjön, Hålen, Refundssjön, Sällsjön, & Ockesjön, Jemtland	Olsson	Olsson 1893 : 17
Salmo trutta	Murman-Küste	Zool. Mus. d. Kais. Akad. Wiss., Petrograd	Linstow 1910 : 281
Salmo umbla	.....	M. C. V.	Diesing 1850 : 591
Salmo umbla	.....	Zschokke	Zschokke 1884 : 21
Coregonus fera	.....	Zschokke	Zschokke 1884 : 21
Coregonus lavaretus	Lakes Störsjön and Nälden	Olsson	Olsson 1893 : 17

HOST	LOCALITY	COLLECTOR	AUTHORITY
Coregonus oxyrhynchus maraena	Warberg	Olsson	Olsson 1867 : 53
Trutta fario	Genfersee, Basel	Zschokke	Zschokke 1896 : 776
Trutta lacustris	Rhine R., Basel	Zschokke	Zschokke 1896 : 776
Trutta lacustris	Bodensee	Hofer	Hofer 1904 : 221
Trutta salar	East Prussia	Muehling	Muehling 1898 : 35
Trutta trutta	Warnemünde	Zschokke	Braun 1891 : 55
Trutta variabilis	.....	Zschokke	Zschokke 1884 : 21
Thymallus vulgaris	.....	Zschokke	Zschokke 1884 : 21
Thymallus vulgaris	Störsjön, Jemtland	Olsson	Olsson 1893 : 17
Thymallus vulgaris	Baikal-See	Zool. Mus. d. Kais. Akad. Wiss., Petrograd	Linstow 1903 : 20
Esox lucius	.....	Zschokke	Zschokke 1884 : 21
Perca fluviatilis	.....	Zschokke	Zschokke 1884 : 21
Osmerus operlanus	Bönan, Gestricia, Gulf of Bothnia	Olsson	Olsson 1893 : 17
Clupea harengus	Ostsee	Schneider	Schneider 1902 : 28
Lota vulgaris	Störsjön, Jemtland	Olsson	Olsson 1893 : 17
Lota vulgaris	Dvina-Fluss	Danilevskij	Linstow 1903 : 20
"Trout"	Loch Tay	Williamson	Scott 1909 : 78
Salmo salar	St. Andrews, N.B., Bay of Fundy	Cooper	Cooper (the present paper)
Cristivomer namaycush	Giants Tomb Id., Georgian Bay, L. Huron	Cooper	Cooper (the present paper)
Cristivomer namaycush	Port Credit, Ont., Lake Ontario	Cooper	Cooper (the present paper)
Cristivomer namaycush	L. Temagami, Ont.	H. B. Ward	Cooper (the present paper)
Cristivomer namaycush	Charlevoix, Mich.	H. B. Ward	Cooper (the present paper)
Cristivomer namaycush	Pentwater, Mich.	H. B. Ward	Cooper (the present paper)
"*Lota lota*"	Charlevoix	H. B. Ward	Cooper (the present paper)
Lota maculosa	Port Credit	Cooper	Cooper (the present paper)
Lota maculosa	Potaganissing, and Sitgreaves Bays, L. Huron	G. R. LaRue	Cooper (the present paper)
Lota maculosa	Charlevoix, Mich.	Cooper	Cooper (the present paper)
Coregonus clupeiformis	Giant's Tomb Island	Cooper	Cooper (the present paper)
Coregonus clupeiformis	Potaganissing Bay, L. Huron	G. R. LaRue	Cooper (the present paper)
Salvelinus fontinalis	Harrietta, Mich.	G. R. LaRue	Cooper (the present paper)

This species, originally given the specific name of *Taenia crassa* by Bloch (1779:545), was on the one hand confused with *A. rugosum* and on the other hand given the new name *Taenia proboscis suilla* by Goeze (1782:410 and 417, resp.) according as it was found in Gadus or in *Salmo salar*. This confusion was evidently due to the fact that the latter followed Pallas (1781) in calling it *T. tetragonoceps*; for, as he said, "Pallas setzt ihn mit Recht l.c. unter die neuen Arten. [In the footnote, he considered that *T. tetragonoceps* Pallas, *Taenia crassa* Bloch and *T. capite truncato* Bloch were all synonymous]. Er hat ihn in verschiedenen Fischen, im Rhein- and Elb-lachs, auch in kleinem Lachs (Eriox) am grössten im Babeljau, im Dorsch, in Schollen und Aalen; der Graf von Borke in der Teufelsmoraene und Meergrappe; D. Bloch in der Madui-Moraene und im Rheinlachs gefunden." But in spite of this, he expressed doubt on the synonym of the forms from the Gadidae and from the Salmonidae in the next paragraph: "Da aber die Zeichnungen des Pallas von der Abbildung des D. Blochs von diesem Wurm, so sehr verschieden sind; und die letztere die nämliche ist, die mir der Graf von Borke von dem Fischwurm aus dem Aal zugeschickt hat; so vermuthe ich fast, dass es dennoch verschiedene Arten sind;" and immediately supported this contention by comparing Loewenhoek's "Vermes multimembres ex Anguilla" (vide supra = *B. claviceps*) with Palla s form and pointing out differences. Elsewhere (p. 417) he described under the name "Der Schweinrüssel *Taenia Proboscis Suilla*: articulis foliaceo sinuosis." from *Salmo salaris* L. what was without doubt the *B. proboscidea* of later writers. Goeze's diagnosis of this form is as follows:

"Vom Graf von Borke aus einem siebenpfundigem Lachs (*Salmo salaris* L.). Besonders in den Blinddarmen. Der Kopf wie ein Schweinsrüssel, mit vier länglichten flachen Saugblasen. Gleich hinter dem Kopfe, ohne Hals, die Blätterförmigen ausgeschweiften Glieder. Ich will nicht mit Gewissheit behaupten, dass dies eine ganz besondere Art sey. So hatte ihn der Graf von Borke gesehen und der Kopf unterscheidet sich von andern. Diese Zeichnung, die ich hier liefre, war auch dem Hr. D. Bloch, mitgetheilet."

The explanation (p. 418) of the figures 1 and 2, Table XXXIV, here referred to, indicate, incidentally, that he considered the bothria to be lateral instead of dorsoventral in position. Rudolphi (1810:39, 46, resp.) gave the first diagnoses of the two species, viz., *B. proboscideus* and *B. infundibuliformis*, which were later united by Zschokke (1884:21) and Matz (1892:110) into one species, now known as *A. crassum*. Rudolphi's later (1819:137) condensed diagnoses are here given for the sake of comparison:

"2. Bothriocephalus proboscideus R.

B. capite bothriisque marginalibus oblongis, collo nullo, corpore depresso medio sulcato, articulis brevissimis, antrorsum attenuatis."

"5. Bothriocephalus infundibuliformis R.

B. capite bothriisque oblongis, collo nullo, articulis variis, primis rugaeformibus, sequentibus subinfundibuliformibus, reliquis brevioribus." In the same work (pp. 472, 473) he pointed out resemblances between these two species in that, as regards *B. proboscideus*, "Specimina maxima in intestinis *Salmonis*

Huchonis reperta, quae Bremserus mecum communicavit ad speciem insequentem (praesertim parte anteriore) transitum faciunt;" and under *B. infundibuliformis*, the following species, concerning the same specimens: ". . . quae parte anteriore cum B. proboscideum arguunt." Leuckart (1819:38, 42) accepted Rudolphi's two species and gave good figures of the scolices and anterior ends of the same; but recognized two forms of *B. proboscideus*, viz.,

"a. Collo nullo; corpore medio sulcato.
Habitat in Salmonis salaris appendicibus pyloricis.
b. Collo brevissimo; corpore medio non sulcato.
Habitat in Salmonis Huchonis intestinis."

He further pointed out and corrected the errors of Pallas, Bloch and Goeze regarding the scolex, and concerning *B. infundibuliformis* said : "Kömme *B. proboscideus* am nächsten, ist aber gewiss eine von ihm verschiedene Art, obgleich Bremser . . . sagt, dass er beide Arten nicht gern trennen mögte." Bellingham (1844:252) was evidently the first to comment on the relation between the number of individuals of this species and the condition of the host, when he said, "I have found the *B. proboscideus* in such numbers in the intestines and pyloric appendages of the *Salmo salar* as almost completely to block up these parts, which contained nothing besides but a white tenacious mucus. The fish in which they were most numerous were amongst the finest in the market; which would help to prove, that in these animals at least, the presence of entozoa in the alimentary canal is not to be regarded as the result of disease." He pointed out the great variation due to different states of contraction or relaxation of the scolex and segments and also that *B. infundibuliformis* from *Salmo trutta* " . . . resembles generally the *B. proboscideus*, but differs from it in some respects." While Olsson (1867:53) and Van Beneden (1871:69) found only *B. proboscideus*, others recognized Rudolphi's two species; so that it remained for Zschokke (1884:21-25) to compare the two species in detail and point out that they must be considered only different forms of the same species. Later investigations into the anatomy by Matz (1892:110), who, however, studied only the *proboscideus* form from *Trutta trutta* and *Salmo salar*, were considered to have established this contention, altho Olsson (1893: 17) still reported both of the older species with some doubt as to the use of the name *B. infundibuliformis*. Blanchard (1894:701), Ariola (1896:280), and Riggenbach (1896:223) evidently accepted only the combination *Abothrium crassum* (Bloch) which is now generally accepted. Ariola (1900:433), however, called the species *Bothriotaenia proboscidea* (Batsch), thus disregarding the fact that Batsch (1786:212) renamed Bloch's *T. crassa*.

In general appearance the material studied agreed with the descriptions of both *B. proboscideus* and *B. infundibuliformis* of the early writers; for the former type from *Salmo salar*, the Atlantic salmon, would at first sight be considered to belong to a different species from those taken from the fresh-water hosts. The largest of the latter was one from a specimen of *Cristivomer namaycush*, which measured 856mm. in length by a maximum breadth of 3mm., while the largest from the salmon measured 754mm. in length, 6mm. in maximum

breadth and about 2mm. in thickness. One from *Coregonus clupeiformis* measured 292 by 1.8mm. and another 185 by 2mm., while those from *Lota maculosa* were all small, fragmentary and mostly immature. The dimensions are according to Lühe (1910:27) about 300mm. in length by about 1.5 to 3.5 in breadth; to Zschokke (1884:23) 350 by 4mm.; and to Ariola (1900:435) 250 to 400 by 2 to 4mm. Thus it is seen that as regards size the two forms are more nearly alike in Europe than here. Consequently one is not surprised to read in the comparison by Zschokke, "En effet je trouvais souvent dans le même poisson, même dans le même appendice pylorique des exemplaires dont les uns se rapprochaient évidemment du *Bothriocephalus proboscideus*, tandis que les autres présentaient les caractères de l'*infundibuliformis*. Souvent aussi les caractéres des deux espèces étaient réunis sur un seul individu, par exemple le cou assez prononcé avec des proglottis en forme de bâtons, ou point de cou avec les proglottis *infundibuliformes* bien caracterisés."

In preserved material the scolex assumes a great variety of shapes, from the much elongated form with the "neck" of Olsson (1893:17) and earlier writers shown in figure 37, to that from *Salmo salar*, shown in figure 39. Altho the latter is much the largest and apparently quite different from the former, scolices quite like it excepting for size were seen in specimens from the lake trout, and all stages between these two extremes were observed. The form with the neck, it may be said, is much more common in the youngest strobilas and plerocercoids (Figs. 53, 54). Regarding this structure Zschokke (1884:24) said that, "à l'état de forte contraction le cou disparaît presque complétement." Those from *Lota maculosa*, the ling, need special mention since, as shown in figure 38, the terminal disc and anterior half of the organ of fixation is in many instances greatly swollen to form a sort of pseudoscolex which is usually found imbedded in the walls of the pyloric ceca of the host or often simply protruding into the lumina of the ceca. But this modification was found only in the older strobilas; in the younger chains the scolex is as shown in figures 41, 42, which are drawn to the same scale. The largest with this first form of scolex was 30mm. in length by 1.2 in breadth, while the shortest with the swollen end was 20 by 1.0mm.; so that somewhere between the lengths of 20 and 30mm. the imbedding of the scolex with the concomitant enlargement of the terminal disc takes place. Several intermediate stages were seen, and the swollen scolices were varied in shape and degree of intactness. The latter might seem to point to the condition being due to mechanical or physical means, but this is offset by the fact that the material was in good histological condition when sectioned.

The segments also vary considerably in shape, the first ones being in specimens from fresh-water hosts distinctly cuneate or infundibuliform and slightly broader than long, the middle ones relatively broader and shorter, and the posterior segments especially in the older chains very short and crowded. Furthermore, in larger and older strobilas of the fresh-water form the posterior kind of segment, that is, the very short broad form, is found relatively farther forward, and the hinder end of the same quite similar, excepting for size, to

the worms from the salmon. In the latter the segments, as shown in figure 39, are at first short and broadly cuneate and at once become still shorter and more crowded. On the whole the marine form of the species appears to be constantly in a better state of nutrition than the fresh-water form. As the measurements given here indicate, the strobila is much wider and thicker and the scolex much larger; but what attracts one's attention at first sight is the clear-cut nature of the scolex and segments of this, the *proboscideus* type, which led Bellingham (1844:252) to describe it as "a very beautiful species," as compared to the other form. In the latter the posterior, much-crowded proglottides, especially, are often irregularly swollen transversely or longitudinally so as to present appearances in many cases quite like those to be seen in *A. rugosum*. Much of this may, however, be due to osmotic action when the worms are near the point of death with the possible low resistance of the body-wall of the posterior segments when growth and development have gone on to such a stage that they are little more than sacs filled with eggs. As pointed out by various writers the posterior borders of the segments are provided in the median line and on both surfaces with a distinct notch or emargination, which together form a longitudinal groove on each face of the chain. This is quite pronounced in the strobilas from the salmon but often not so marked in those from the whitefish, lake trout and ling. In these it is confined more to the posterior stretches of the segments and greatly exaggerated by the above mentioned irregular swellings which, however, do not cross the longitudinal groove formed by these notches. Often this groove may be present in the segments close to the scolex and again in posterior ones but absent in the middle stretches, where, of course, the emarginations are either almost absent or all but obliterated by the degree of relaxation. On the contrary, Olsson (1893:17) often found the groove only in the middle portions of the *infundibuliformis* form. Many specimens also show the condition described by Leuckart (1819:42) when he said, "Die hinteren Ränder dieser Glieder scheinen allerdings etwas verdickt und stehen an den Körperrändern sehr hervor." In the anterior segments of considerably relaxed or especially young strobilas something of the manner of segmentation can be seen. This was found to take place much as in the genus Bothriocephalus, altho the writer was not able to distinguish the primary segments to his satisfaction. What was considered to be such is shown in figure 64, a sketch of segments beginning 27mm. from the anterior end of the strobila in question. The idea of dominance of the anterior portions over the posterior portions in segmentation, as brought out under *B. scorpii*, is here shown very nicely. In the *proboscideus* type of strobila the same method of subdivision was followed in the anterior segments, altho with greater difficulty on account of the fact that the segments are so closely crowded in the longitudinal direction. Olsson (1867:53) noticed the subdivision of the segments producing an alternation of larger segments with smaller ones, and he considered it to be an *articulatio spuria* similar to that described by Wagener (1854:69) for *Amphicotyle heteropleura* and by Krabbe (1865:384) for *B. scorpii* and other species. Later Olsson (1893:17)

states that transverse divisions occured in *B. infundibuliformis* as well as in *B. proboscideus*. Finally, as regards the external features, it should be noted that the posteriormost, yet ripe proglottides of the smaller strobilas from the fresh-water hosts are quadrate in shape, often as long as broad, and usually somewhat narrower than the mature segments ahead. These, as stated by Olsson (1893:17), show practically nothing more in the way of reproductive organs than the lobed uterus-sacs. The following measurements of the scolex are given for the sake of comparison:

HOST	*Salmo salar*	*Cristivomer namaycush*		*Lota maculosa*
Length	1.01mm.	0.70mm.	0.87mm.	0.71mm.
Width of terminal disc	0.74	0.42	0.47	0.41
Width of bothrium (middle)	0.94	0.52	0.38	0.60
Length (laterally)	0.88	0.70	0.74	0.64
Depth of terminal disc	0.56	0.33	0.44	0.36
Depth posteriorly	1.25	0.40	0.55	0.68

The anatomy of the species was studied by Matz (1892:110), later writers referring to his work, altho Zschokke (1884:24), Lönnberg (1889:35) and Olsson (1893:17) made some valuable contributions, while Lühe (1899a and 1900a) dealt with it from a comparative standpoint. Most of them, however, confined their attention almost entirely to the reproductive organs.

The cuticula, from 4 to 5μ in thickness, is divisible into two layers besides the basement membrane, an outer and darker occupying about one-third of the thickness of the whole, and quite smooth, and an inner, quite light layer. It is slightly modified on the posterior borders of the segments to form minute spinelets which are evidently formed by the splitting of the somewhat thickened outer layer. This modification is, however, not so well marked as in other species. The subcuticula, from 60 to 100μ in thickness, extends from the cuticula to the longitudinal muscles, thus occupying the outer one-half of the cortex. Its nuclei are confined to its inner half, thus leaving the outer ends of the cells free. The whole tissue requires good fixation and preservation to show these features which in the older proglottides and longer strobilas are otherwise affected by the general degeneration coincident with the development of the enormous number of eggs produced by this species. And it should be stated here that this is more applicable to the large marine form than to those from fresh-water hosts. So far as the writer is aware no calcareous bodies have been described for this species. They were found only in the smallest strobilas with a maximum diameter of 15μ. The parenchyma is in the form of a very fine reticulum, the spaces of which form the bulk of the tissue.

Unlike *A. rugosum* the longitudinal muscles of the parenchyma are not arranged in fasicles; nor do the transverse fibres form a septum between even the anterior segments. The latter are often more numerous towards the posterior end of the segments, as are the sagittal fibres, but they do not prevent

the testes from being continuous from proglottis to proglottis, nor the anterior end of the uterus-sac from protruding considerably into the proglottis immediately ahead. In the material from *Lota maculosa* the myoblastic nuclei and protoplasm of the sagittal fibres are almost as prominent as in *A. rugosum.* There is a weakly-developed series of external longitudinal muscles arranged in relation to the posterior borders of the anterior segments as described above. The musculature of the ordinary form of the scolex is typical. Transverse or circular, sagittal or radial, and longitudinal muscles are about equally developed, the latter entering the base of the organ in scattered groups, altho not distinctly fascicled, and extending to the tip. A series of well developed longitudinally arcuate fibres, arranged around the border of the terminal disc is present, quite as described by the writer elsewhere (1914a:92) for *Haplobothrium globuliforme.* In the enlarged scolex from *L. maculosa*, altho the general arrangement of the musculature is retained, the number of fibres is greatly diminished and the whole ensemble indicative of not a little degeneration. This is emphasized by the fact that in the unenlarged portion of the organ there is to be seen in sections a deposition of material which stains much like that described above for the young pseudoscolices of *A. rugosum.* This is absent, however, from the enlarged terminal portion.

In the form from the salmon the chief nerve strands reach a maximum dorsoventral diameter of about 100μ by a transverse diameter of 40μ. They are located at the extreme lateral limits of the medulla, all of the testes coming between them, as pointed out by Lühe (1900a), and pass dorsal to the inner end of the cirrus-sac and consequently to the vagina, as mentioned by Matz (1892:112). In the scolex the chief strands enlarge at the level of the border of the terminal disc to form two ganglia which are united by a small transverse commissure, the whole arrangement being quite comparable to that present in *B. cuspidatus.*

Zschokke (1884:25) said that "Les canaux excréteurs sont parallèles et voisin des bords lateraux," while Fraipont (1881:12) described the system as follows: "La vesicule terminale est petite. Le système des *canaux descendants* est fort compliqué; ils fournissent des branches latérales de volume très variable; les unes volumineuses, les autres excessivement grêles. Les branches forment un réseau à mailles très inégales. Des canaux très fins peuvent partir directement des gros troncs. Dans la tête, les canaux descendants forment un reticulum très compliqué. Cretaines ramifications très fines se terminent par des entonnoirs ciliés identiques à ceux du *B. punctatus.*" In mature proglottides about six of these descending canals are seen on each surface of the strobila, as stated by Matz, those on the ventral surface, altho of varying size, being constantly the largest. The outermost of these passes ventral to the cirrus-sac, while the corresponding dorsal one is much more median in position. All of the vessels lie just within or sometimes among the inner transverse muscles but not so much among the vitelline follicles as Matz found. In the first segments these twelve canals become reduced to three or four, irregularly arranged on each side of the median sagittal plane, of which one or two may

course outside of the nerve strand for considerable stretches. Only one large vessel, just within the nerve strand, passes into the base of the scolex on each side. These two are quickly reduced in size and disappear at about the middle of the scolex. In the youngest plerocercoids, such as shown in figure 50, there was seen at the posterior end a cuticular sac or invagination about 45μ in length by 10μ in diameter, much resembling an excretory vesicle. But since no vessels connected with this structure as in *A. rugosum*, its nature was not satisfactorily determined. On the other hand, the vessels of a young strobila which had evidently just lost some segments did not open on the concave posterior end but were lost in the parenchyma some distance from the end after considerable anastomosing.

The earliest traces of the reproductive rudiments appear in the marine type about 45mm. from the tip of the scolex while the first eggs are to be seen in the uterus 63mm. from the same point. The same data for a considerably relaxed strobila from *Coregonus clupeiformis* are respectively 62 and 225mm. Olsson (1893:17) found the first testes to appear in a 200mm. strobila from *Salmo alpinus* 95mm. from the anterior end, while 20mm. farther the uteri began to show. Depending a great deal on the amount of relative contraction of the proglottides, the genital cloaca is situated from one-third to half way along the margin of the segment, altho Matz (1892:112) stated that its location was between the first and second thirds of the edge of the proglottis. He also said that they (? the cirrus-sacs) always opened on the left margin of the strobila; but Lühe (1899) corrected this error by stating that altho they are situated on one side for long stretches, in reality they alternate from side to side. The writer also found them to be irregularly alternating but unilateral thru many proglottides. In one strobila from a whitefish, for instance, they were found to be arranged as follows, the numbers representing the numbers of proglottides in which they are on the same side before changing to the opposite margin: 16, 3, 2, 5, 41, 21, 19, 7, 7, 8, 13, 3, 4, 11, 28, 9, 7, 9, 35, 10, 26, 9, 7, 9, 35, 11; while in a stretch of gravid proglottides from *Cristivomer namaycush*, the lake trout, the data are: 27, 2, 80, 4, 3, 2, 13, beyond which the cirrus-sacs had so degenerated that it was found impossible to follow them with satisfaction in the toto preparations. Zschokke (1884:25) erroneously described the cirrus-pouch as being ". . . située vers le milieu de la face ventrale de chaque proglottis," while "L' orifice femelle se trouve en dessous, vers le bord postérieur du proglottis," thus leading Lönnberg (1889:35) to establish the new species *B. suecicus* which Matz (1892:111) considered with obvious justification to be synonymous with his *B. infundibuliformis*, or *A. crassum* as it is now known. The cloaca itself is tubular, from 50 to 60μ in depth in the fresh-water from and about 175μ in the marine form. In either case there is no sharply separated hermaphroditic duct, the cirrus and vagina opening very close together at the bottom of the pore, the latter constantly ahead of and more or less ventral to the former.

Matz stated that the testes were about 300 in number, 72μ in size, and extended from the median line to the lateral nerves, while Lühe (1900a) described

them as being between the uterus and the marginal nerves as in *B. imbricatus*. In the present study they were found to pass to the median line and dorsal to the uterus-sac in the anterior portion of the proglottis but to be prevented from doing so posteriorly by the ovary and the ducts in its immediate neighborhood. They are not all in the same horizontal plane but arranged in two or three pseudostrata (Fig. 92). Their number is from 40 to 150 in each proglottis with an average of 90, and their dimensions from 95 to 115μ in depth by 70 to 100 in transverse diameter, being roughly circular in frontal sections. The vas deferens forms an elongated mass of coils of quite the same shape and arrangement with the fewer coils before entering the cirrus-sac as in *A. rugosum*. Its dimensions are 0.35 to 0.60 by 0.15 to 0.18mm. In the proximal one-third to one-half of the cirrus-sac the male duct forms a mass of coils, the ejaculatory duct, which may or may not become enlarged with sperms to form at least a temporary inner seminal vesicle, while in the distal half of the pouch it continues in an almost straight course as the cirrus proper with a maximum diameter of 20μ. The cirrus-sac varies in dimensions from 130 to 220 by 60 to 105μ in the fresh-water form and 255 to 380 by 120 to 150μ in the form from *Salmo salar*, and is ovoid in shape with the smaller end, often quite pointed, towards the genital cloaca. Matz gave the length of the cirrus-sac as 255μ for the form from the European salmon and salmon trout. The wall is comparatively thinner and there are fewer parenchymatous nuclei around it or within it among the conspicuous retractor muscles than in *A. rugosum*.

The vagina opens constantly ahead of the cirrus and more or less ventral to it as pointed out by Matz (p. 112). From this point it bends backward and gradually downward, thus making a bow which lies below the coils of the vas deferens, and then courses mediad parallel to the anteroventral border of the latter. Near the median line, however, it again rises to pass over the lateral border of the ovary before gaining the oviduct. There is thus a broad ventral bow to the vagina, which, contrary to Lühe's statement, is more median than in *A. rugosum*. Opposite the cirrus-sac the vagina may be found enlarged to a diameter of 35μ. The ovary is quite irregular or only very roughly kidney-shaped as stated by Lühe (1900a), and has a maximum diameter in the marine form of 0.8mm. by a length of 0.13mm. As in *A. rugosum*, there is a very broad isthmus, with the posterodorsal part of which the oviduct is connected by the oocapt which has a diameter of 40μ. The oviduct receives the vagina in the median coronal plane. Usually two small vitelline ducts passing along the ventral floor of the medulla unite in the median line to form a common duct which is not enlarged to form a reservoir; but in the material from Lota two others were seen to unite dorsally to form another common duct, while the ventral duct formed a number of anastomoses with its tributaries before uniting with the oviduct. Matz described the vitelline follicles as irregular in shape, discontinuous from proglottis to proglottis and located among the longitudinal muscles, there being about 29 "on the surface," presumably in transverse sections. The writer likewise found them to be quite irregular in shape and to range in location from among the inner longitudinal muscles to distinctly out-

side of them and even among the subcuticular nuclei in the *proboscideus* form. In toto mounts of anterior segments they may be seen to be quite discontinuous and, as pointed out by Lühe (1900a), arranged in two lateral fields on each surface, there being a few, however, in the median ventral line. The combined ootype and shell-gland is a small inconspicuous compact structure lying close to the dorsal wall of the medulla as in *A. rugosum*. The uterine duct also takes only a very few coils before expanding into the capacious uterus-sac. Matz described the latter as being not round as in *B. scorpii* and *B. claviceps*, but pointed towards each side, which points do not disappear when the sac is filled with eggs, while Lühe (1910:17) repeats this statement. In the material studied by the writer only the young uterus-sacs, much elongated in the transverse direction, were found to be pointed laterally, but the mature structures, i.e., when filled with eggs, distinctly rounded or only very broadly pointed in some cases (Fig. 77). In dorosoventral view the sac varies in shape from an elliptical or quadrate, lobed organ, filling up most of the proglottis in the fresh-water form, to a transversely much elongated cavity in the *proboscideus* form, so enlarged in mature joints that the strobila in such gravid regions is little else than a tube filled with eggs. The openings are situated in the median line on the ventral surface, each one being just opposite the posterior emargination of the segment immediately ahead.

Matz states that the egg measures 54.5 by 40.9μ, but the writer found them of quite different sizes when removed from gravid segments in the 5% formalin solution in which they were preserved. In general, two sizes were seen, small ones with thicker darker shells and larger ones with thinner lighter shells, but at the same time all intermediate sizes between these forms. Those from the fresh-water form of the species measured 55 to 115 by 35 to 75μ, while those from the form from *Salmo salar* were 45 to 110, by 30 to 75μ, thus showing that so far as the size of the eggs goes, at least these two forms are one and the same species.

So far as the writer is aware the development of the egg of this species has been studied only by Koelliker (1843:91) and later by Braun (1889:668, etc.) in review. Several writers have described various young plerocercoids. The youngest found by Olsson (1867:53) was only 2mm. in length and had only three segments, a neck and several longitudinal spiral excretory canals, of which two extended to the anterior part of the head. The triangular caudal piece of this young strobila had a median sinus posteriorly, thus indicating, perhaps, in the light of the present contributions, that a portion had already diasppeared. Leuckart (1878:605) spoke of the simplicity of the development of the plerocercoid, while Zschokke (1884:27) believed that he had found the larvae of *B. infundibuliformis* in numerous cysts on the outside of the walls of the alimentary tract of *Perca fluviatilis*, *Trutta vulgaris*, *Esox lucius*, *Salmo umbla*, *Thymallus vulgaris* and *Lota vulgaris*. They were also found on the liver, the spleen, the ovaries and the peritoneum of the same fishes, with their scolices ordinarily invaginated and with lengths of from 2 to 6mm. In 1893 Olsson again referred to the plerocercoids and younger strobilas. In *Lota vul-*

garis he found young strobilas, still possessing the rounded caudal piece but no neck, with the habit of invaginating their scolices. In a *Salmo salar* he found on July 4th similar young "scolices" (plerocercoids) not only free in large numbers in the intestine of the host posterior to the pyloric ceca but also present along with the anterior ends of adult strobilas in the ceca themselves. Again in June he found a great many young strobilas in *S. alpinus*. These facts, together with the further fact that the adult worms have been found in the hosts during every month of the year, points to infection of the final host with the pleroceroids at all times of the year. Of chief interest in this connection is the finding by Schneider (1902:28) of young plerocercoids 2 to 7mm. long free in the stomach and intestine of *Clupea harengus membras* L., which he believed to be the young stages of *Bothriotaenia proboscidea* (Batsch), as he called the species. They were found in greater numbers towards the latter part of June than at other times during the summer. Concerning the significance of the location of the larvae in these herring, he said: "Daher muss ich annehmen, dass dieser Fisch nicht der erste, sondern der zweite Zwischenwirth des Bandwurmes ist. Erster Zwischenwirth, in welchem der Wurm sein Cystenstadium durchläuft, muss wohl ein Arthropode (Kruster oder Insectenlarve) sein, der dem Ostseeheringe sehr oft zur Nahrung dient. Falls meine Annahme richtig ist, woran ich nicht zweifele, das *Clupea harengus membras* L. derjenige Zwischenwirth ist, mit dem der Ostseelachs direct die Larven von *B. proboscidea* in seinen Darmkanal aufnimmt, so erklärt sich leicht das Zustandekommen solcher Wasserinfectionen, wie sie an den Ostseelachsen beobachtet werden." Lühe (1910:12) briefly reviewed the findings of these bothriocephalid larvae in various hosts up to date and pointed out that those of *Diphyllobothrium latum* have often been confused with those of *A. crassum* and that in many cases it is doubtful whether either was certainly at hand. Ward (1910:1184) reported the species from *Salmo salar sebago* and *Cristovomer namaycush*, but was unable to throw any light on the life-history altho he investigated the Sebago smelt as the possible intermediate host. No larvae were found in the latter, but concerning the infection of the final host, he said: "This is worthy of note that all of these parasites were full grown; not a single specimen was found which was not discharging ripe proglottides. Consequently the infestation must have taken place somewhat earlier in the year." The youngest lots of material studied by the writer were two taken from *Lota maculosa* from Lake Ontario, off Port Credit, near Toronto, on Nov. 5 and 8, 1912, and one from the intestine of a young *Cristovomer namaycush* from the same locality on the latter date. The lot from the lake trout contained all stages from that shown in figure 50 to the largest which by comparison with adult specimens from the same host were found to belong to this species. While no stages were found between that shown in figure 52 and that shown in figure 50 altho two others were only very slightly larger than the latter, it seems reasonable to consider the latter itself to belong to this series and to represent the earliest stage of the same. Figures 53 and 54, two later stages, are given to show the manner of beginning of the segmentation and the early

dropping off of two or more very immature segments from the hinder end. The first indication of this is probably represented in figure 52, altho the strobila in figure 53 does not show it. The relative ages, however, of these two is difficult to state definitely since the first one is more contracted longitudinally than the other. On the other hand, two intermediate in length between those shown in figures 53 and 54, were indented posteriorly, thus showing that some of the earliest segments had already been lost. Thus it is seen that at a very early period in the development of the strobila of this species there are lost a few of the first-formed segments in much the same way as the bladder of the cysticercus of the taenioid cestodes is cast off in the final host.

The material studied consisted of lots 86, 87, 88, 303 and 304 from *Salmo salar*, 38a, b, c, d, e, and o, 66, 67, 164, 167 and 192 from *Cristivomer namaycush*, 42 and 166 from *Coregonus clupeiformis*, and 61, 62, 381, and 387 from *Lota maculosa*, in the writer's collection; Ch 26a, Ch 26b, Ch 29a, Ch 29b, Ch34a, T1g, T2q and 17.186 from *C namaycush*, and Ch 13b and Ch 22b from *Lota maculosa*, in the collection of the University of Illinois; and 509c, 511a, 520b, 524a, 525a and 530a from *Salvelinus fontinalis*, 613b and 622d from *Lota maculosa* and 616-620c from "whitefish," in the collection of Dr. G. R. LaRue.

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EXPLANATION OF PLATES

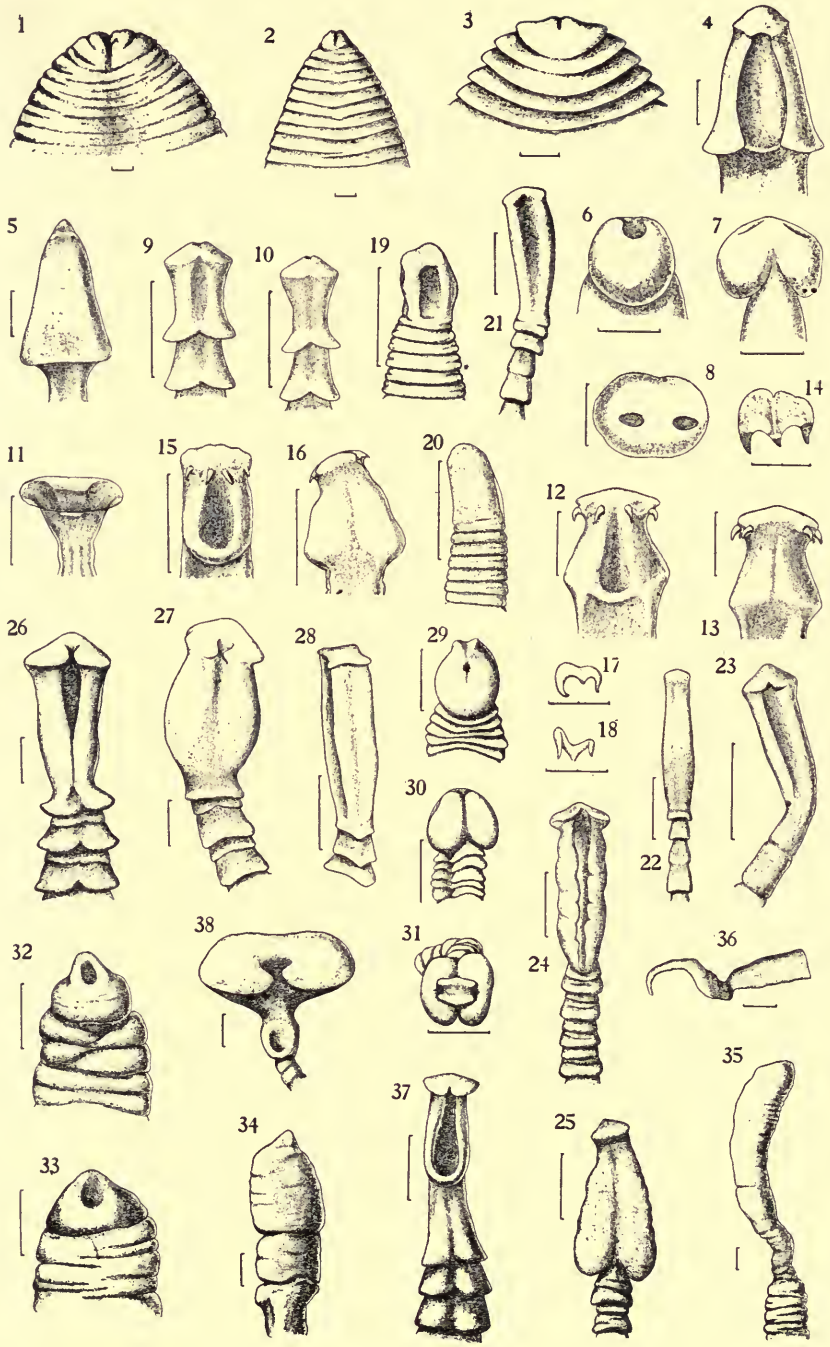
ABBREVIATIONS

bc	bothrial cavity	*ns*	nerve strand
bo	bothrial opening	*o*	ovary
bs	bothrial sphincter	*oc*	oocapt
c	cirrus	*od*	oviduct
cm	circular muscles	*ot*	ootype
cs	cirrus-sac	*p*	proboscis
cu	cuticula	*rs*	receptaculum seminis
cvd	common vitelline duct	*s*	subcuticula
dh	hermaphroditic duct	*t*	testis
dm	dorsoventral muscles	*td*	terminal disc
ec	excretory canal	*tm*	transverse muscles
ed	ejaculatory duct	*ud*	uterine duct
ev	excretory vesicle	*uo*	uterus opening
fa	female atrium	*us*	uterus sac
fd	fertilization duct	*ut*	uterus
g	genitalia	*v*	vagina
ga	genital atrium	*vb*	vestibule
gc	ganglionic cells	*vd*	vas deferens
io	isthmus of ovary	*vg*	vitelline glands
lm	longitudinal muscles	*vo*	vaginal opening
nc	nerve commissure	*vs*	vesicula seminalis

The lines in the figures have the following values: 0.05mm. in figures 63, 67, 105, 106, 107, 108; 0.2mm. in figures 14, 17, 18, 88, 94, 97, 99, 101; and 0.5mm. in all other figures, unless otherwise stated in the explanation of the figure.

EXPLANATION OF PLATE

Fig. 1. *Ligula intestinalis*, anterior end of larva, showing scolex.
Fig. 2. *Ligula intestinalis*, anterior end of adult.
Fig. 3. *Schistocephalus solidus*, anterior end of larva.
Fig. 4. *Marsipometra hastata*, scolex, surficial view.
Fig. 5. *Marsipometra hastata*, same specimen, lateral view.
Fig. 6. *Bothrimonus intermedius*, scolex, surficial view.
Fig. 7. *Bothrimonus intermedius*, same specimen, lateral view.
Fig. 8. *Bothrimonus intermedius*, same specimen, terminal view.
Fig. 9. *Haplobothrium globuliforme*, secondary scolex, surficial view.
Fig. 10. *Haplobothrium globuliforme*, same specimen, lateral view.
Fig. 11. *Cyathocephalus americanus*, scolex, toto preparation.
Fig. 12. Triaenophorus, larva, *robustus* type, surficial view.
Fig. 13. Triaenophorus, same specimen, lateral view.
Fig. 14. Triaenophorus, same specimen, one of the tridents of hooks.
Fig. 15. Triaenophorus, larva, *nodulosus* type, surficial view.
Fig. 16. Triaenophorus, same specimen, lateral view.
Fig. 17. Triaenophorus, same specimen, a trident, terminal view.
Fig. 18. Triaenophorus, same specimen, surficial view.
Fig. 19. *Bothriocephalus claviceps* from *Eupomotis gibbosus*, scolex, surficial view.
Fig. 20. *Bothriocephalus claviceps*, same specimen, lateral view.
Fig. 21. *Bothriocephalus scorpii*, scolex, surficial view.
Fig. 22. *Bothriocephalus scorpii*, same specimen, lateral view.
Fig. 23. *Bothriocephalus claviceps* from *Anguilla rostrata*, scolex, surficial view.
Fig. 24. *Bothriocephalus cuspidatus*, scolex, surficial view.
Fig. 25. *Bothriocephalus cuspidatus*, same specimen, lateral view.
Fig. 26. *Bothriocephalus manubriformis*, scolex, surficial view.
Fig. 27. *Bothriocephalus manubriformis*, same specimen, lateral view.
Fig. 28. *Bothriocephalus occidentalis*, scolex. After Linton.
Fig. 29. *Clestobothrium crassiceps*, scolex, surficial view.
Fig. 30. *Clestobothrium crassiceps*, same specimen, lateral view.
Fig. 31. *Clestobothrium crassiceps*, same specimen, terminal view.
Fig. 32. *Abothrium rugosum*, scolex of young strobila.
Fig. 33. *Abothrium rugosum*, later stage in degeneration of same.
Fig. 34. *Abothrium rugosum*, still later stage.
Fig. 35. *Abothrium rugosum*, pseudoscolex from lumen of pyloric coecum of host.
Fig. 36. *Abothrium rugosum*, pseudoscolex from wall of coecum.
Fig. 37. *Abothrium crassum*, scolex from *Cristivomer namaycush*.
Fig. 38. *Abothrium crassum*, enlarged scolex from *Lota maculosa*.

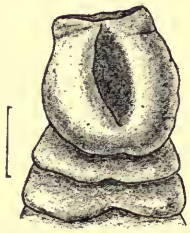


COOPER PSEUDOPHYLLIDEAN CESTODES PLATE I

PLATE II

EXPLANATION OF PLATE

Fig. 39. *Abothrium crassum*, scolex of specimen from *Salmo salar*, surficial view.
Fig. 40. *Abothrium crassum*, same specimen, lateral view.
Fig. 41. *Abothrium crassum*, young scolex from *Lota maculosa*.
Fig. 42. *Abothrium crassum*, same specimen, lateral view.
Fig. 43. *Haplobothrium globuliforme*, primary scolex, toto preparation.
Fig. 44. *Haplobothrium globuliforme*, primary strobila, toto preparation.



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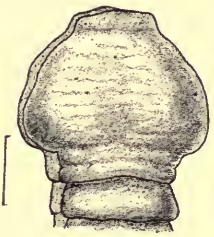

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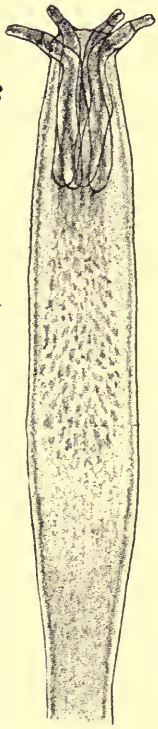

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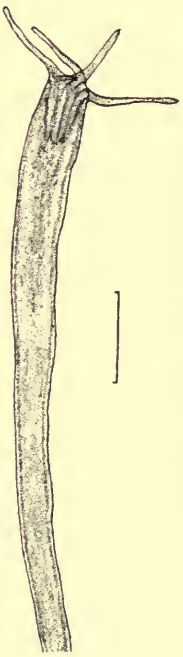

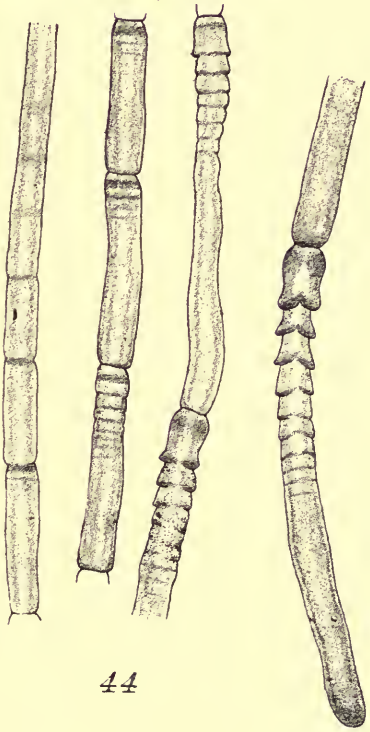

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COOPER PSEUDOPHYLLIDEAN CESTODES PLATE II

PLATE III

EXPLANATION OF PLATE

Fig. 45. *Bothrimonus intermedius*, scolex and anterior end, toto preparation, showing foremost sets of genitalia.
Fig. 46. *Marsipometra hastata*, plerocercoid, surficial view.
Fig. 47. *Marsipometra hastata*, older plerocercoid, surficial view.
Fig. 48. *Clestobothrium crassiceps*, toto of scolex and anterior end.
Fig. 49. *Clestobothrium crassiceps*, toto of young strobila, surficial view.
Fig. 50. *Abothrium crassum*, plerocercoid from *Cristivomer namaycush*, surficial view.
Fig. 51. *Abothrium crassum*, same specimen, lateral view.
Fig. 52. *Abothrium crassum*, young strobila from same host.
Fig. 53. *Abothrium crassum*, older strobila from same host.
Fig. 54. *Abothrium crassum*, still older strobila, showing dropping off of segments posteriorly.

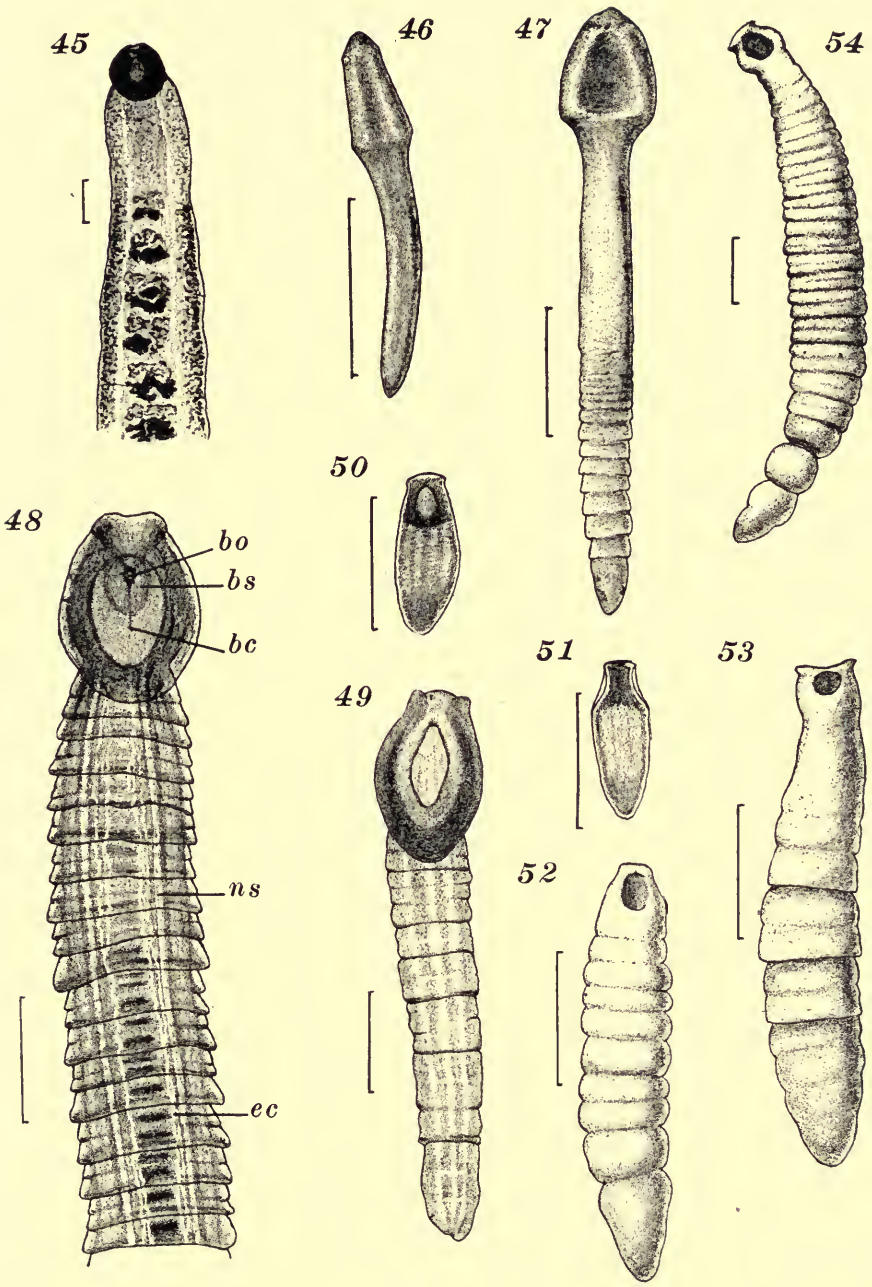
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PLATE IV

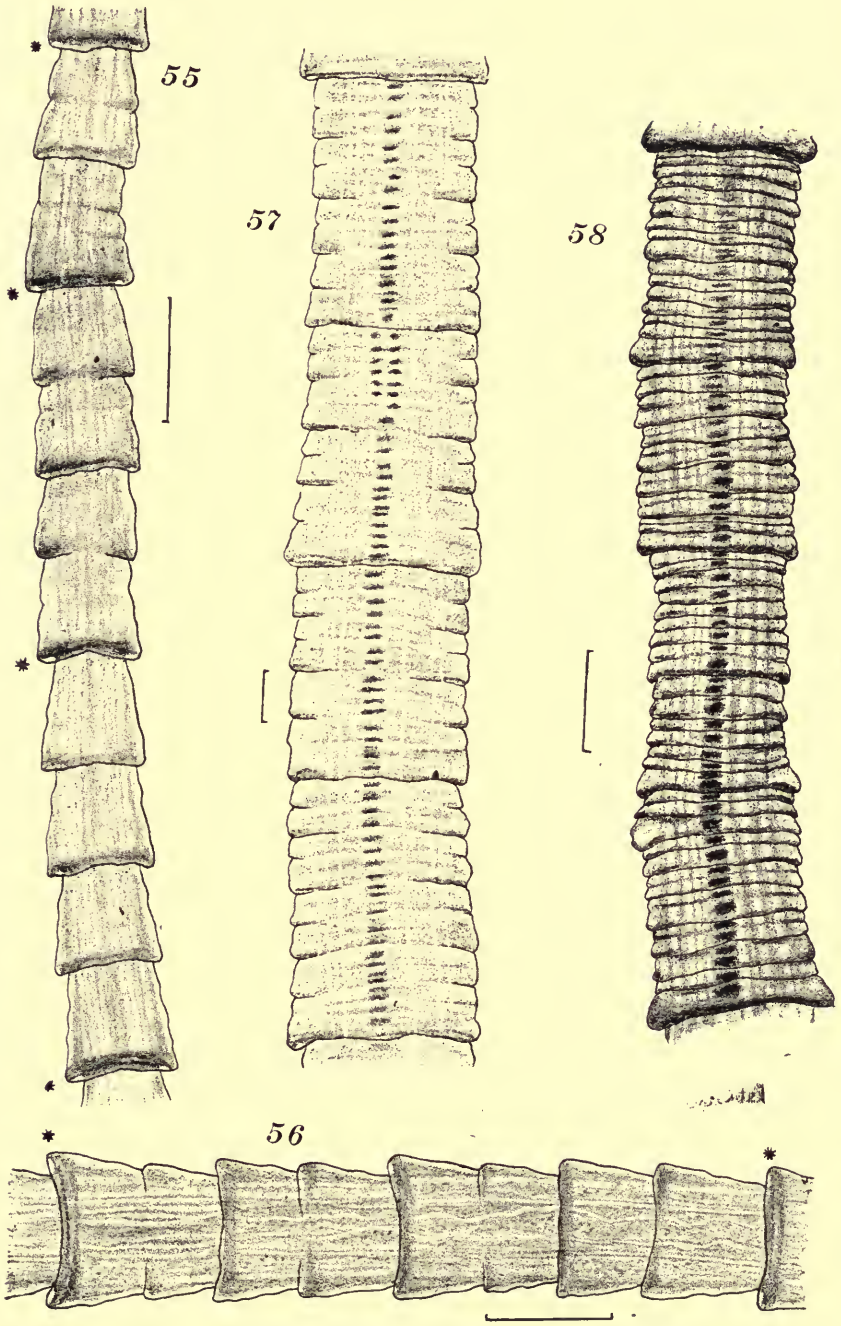
EXPLANATION OF PLATE

Fig. 55. *Bothriocephalus scorpii*, three anterior primary segments, toto preparation. The stars at the side indicate the extent of the segments.

Fig. 56. *Bothriocephalus scorpii*, one farther back, also toto.

Fig. 57. *Bothriocephalus scorpii*, another, showing reproductive rudiments.

Fig. 58. *Clestobothrium crassiceps*, primary segment with reproductive rudiments, toto preparation.

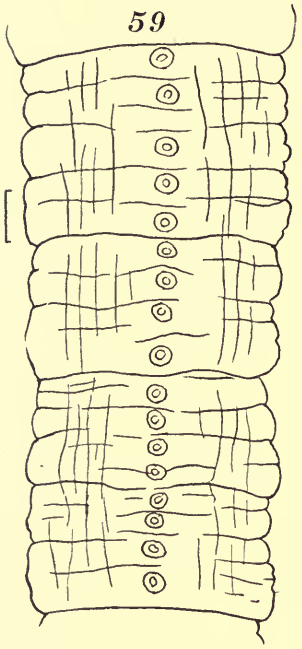


COOPER PSEUDOPHYLLIDEAN CESTODES PLATE IV

PLATE V

EXPLANATION OF PLATE

Fig. 59. *Bothriocephalus scorpii*, outline of mature segments.
Fig. 60. *Bothriocephalus scorpii*, toto of same specimen.
Fig. 61. *Bothriocephalus scorpii*, portion of strobila showing excretory vessels.
Fig. 62. *Bothriocephalus manubriformis*, anterior primary segment.
Fig. 63. *Abothrium rugosum*, terminal excretory vesicle.
Fig. 64. *Abothrium crassum*, anterior segments of strobila from *Coregonus clupeiformis*, toto.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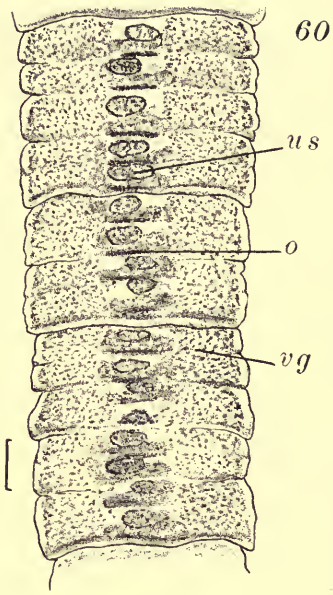
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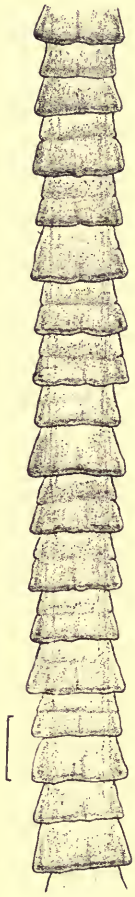
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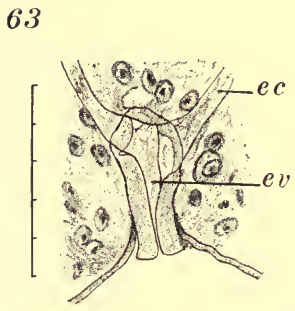
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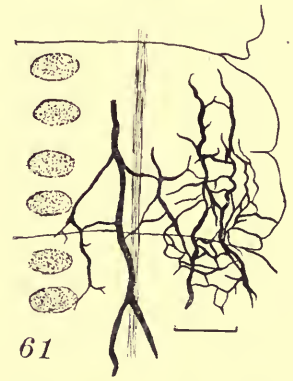
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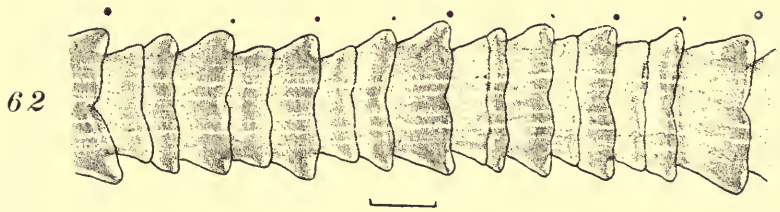
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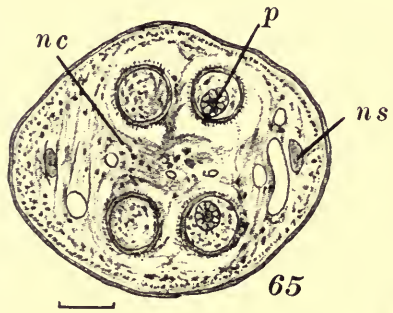
Fig. 65. *Haplobothrium globuliforme*, transection thru primary scolex.
Fig. 66. *Haplobothrium globuliforme*, transection thru the ganglionic mass behind the proboscides. The reference line is 0.1mm. long.
Fig. 67. *Haplobothrium globuliforme*, transection thru a single proboscis bulb.
Fig. 68. *Marsipometra hastata*, toto of ripe proglottis.
Fig. 69. *Bothriocephalus cuspidatus*, transection thru an anterior segment.
Fig. 70. *Bothriocephalus cuspidatus*, toto of ripe proglottides, posterior in deeper optical section.



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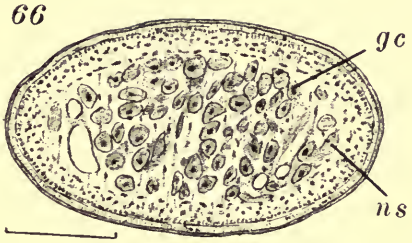

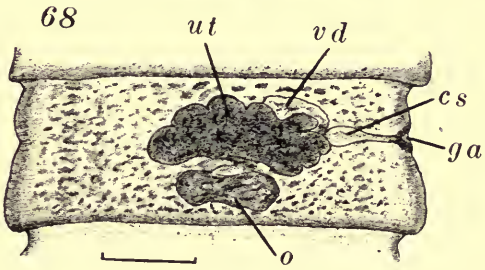

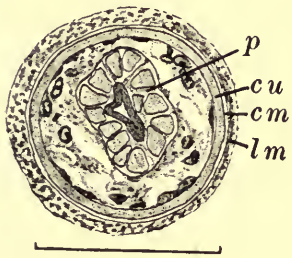

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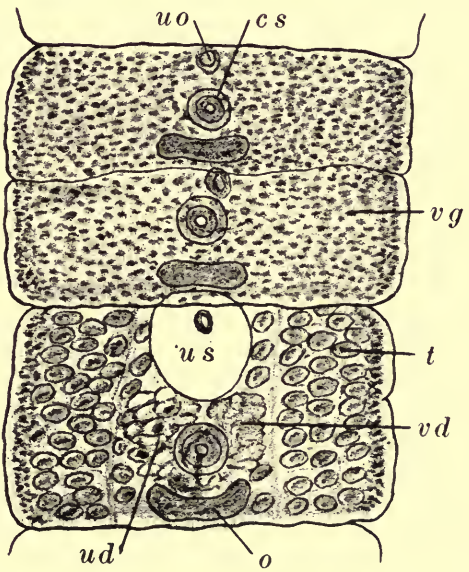

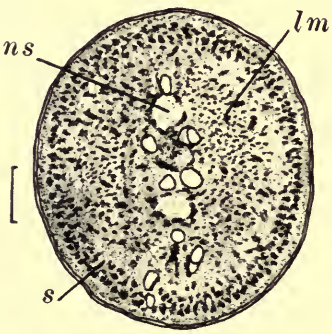

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Fig. 71. *Bothriocephalus scorpii*, toto of two segments.
Fig. 72. *Bothriocephalus claviceps* from *Eupomotis gibbosus*, toto of mature proglottides.
Fig. 73. *Bothriocephalus manubriformis*, toto of mature proglottides.
Fig. 74. *Clestobothrium crassiceps*, segments showing spurious articulations.
Fig. 75. *Clestobothrium crassiceps*, toto of mature proglottis.
Fig. 76. *Abothrium rugosum*, frontal section of mature proglottis.
Fig. 77. *Abothrium crassum*, toto of ripe proglottis of strobila from *Coregonus clupeiformis*.

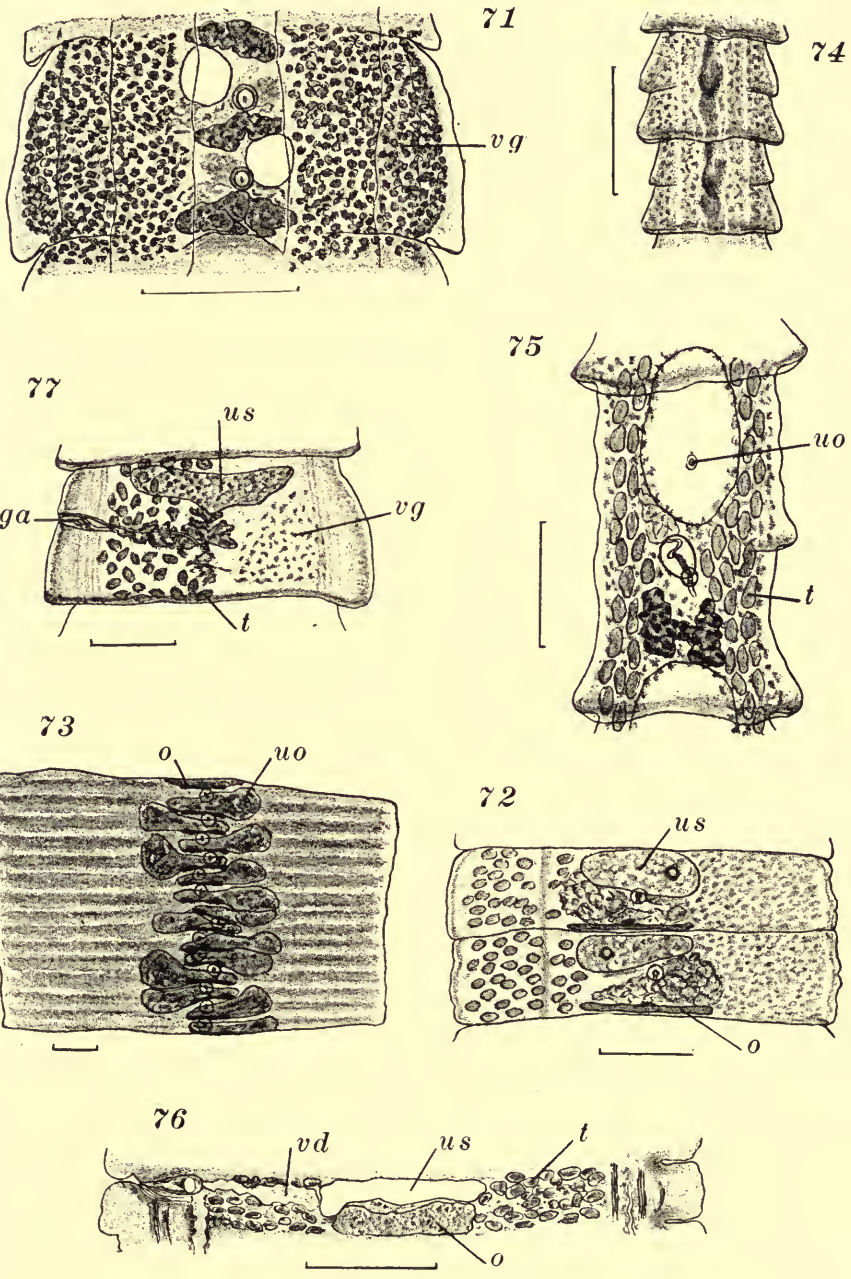
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Fig. 78. *Ligula intestinalis*, median portion of a transection thru the genital cloaca.
Fig. 79. *Schistocephalus solidus*, median portion of transection thru ovary.
Fig. 80. *Schistocephalus solidus*, median portion of transection thru the seminal vesicle and cirrus-sac. The reference line is 0.3mm. long.
Fig. 81. *Bothrimonus intermedius*, transection thru the ovarian isthmus.

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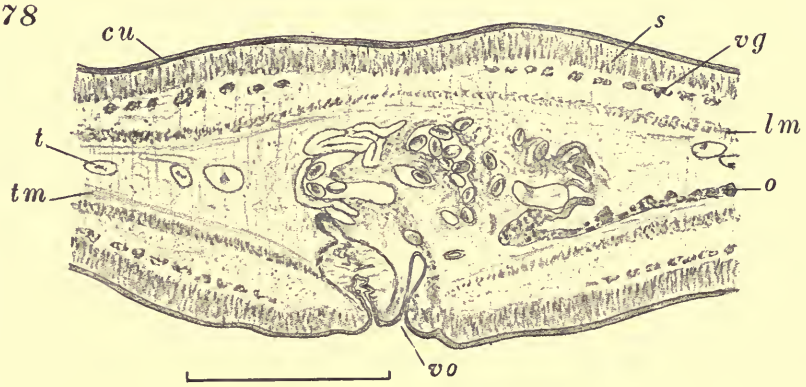

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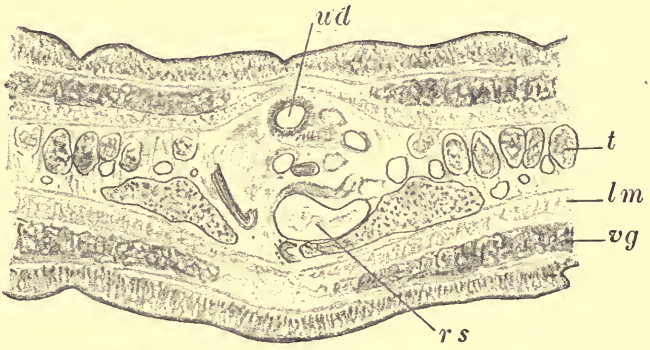

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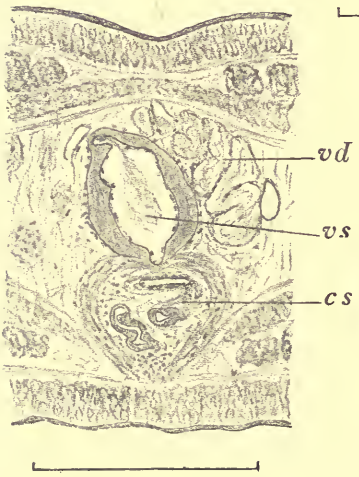

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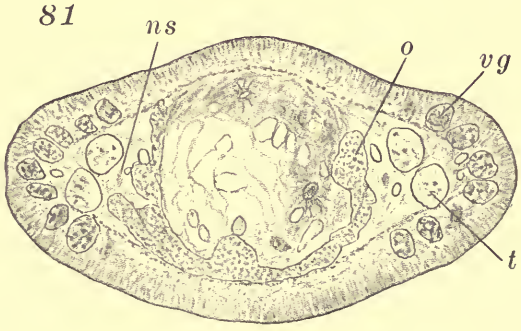

PLATE IX

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Fig. 82. *Cyathocephalus americanus*, transection thru ovarian isthmus.
Fig. 83. *Marsipometra hastata*, transection thru ovarian isthmus.
Fig. 84. *Bothriocephalus scorpii*, transection thru ovary.
Fig. 85. *Bothriocephalus claviceps* from *Eupomotis gibbosus*, transection thru ovary.
Fig. 86. *Bothriocephalus cuspidatus*, transection thru ovary of mature proglottis.

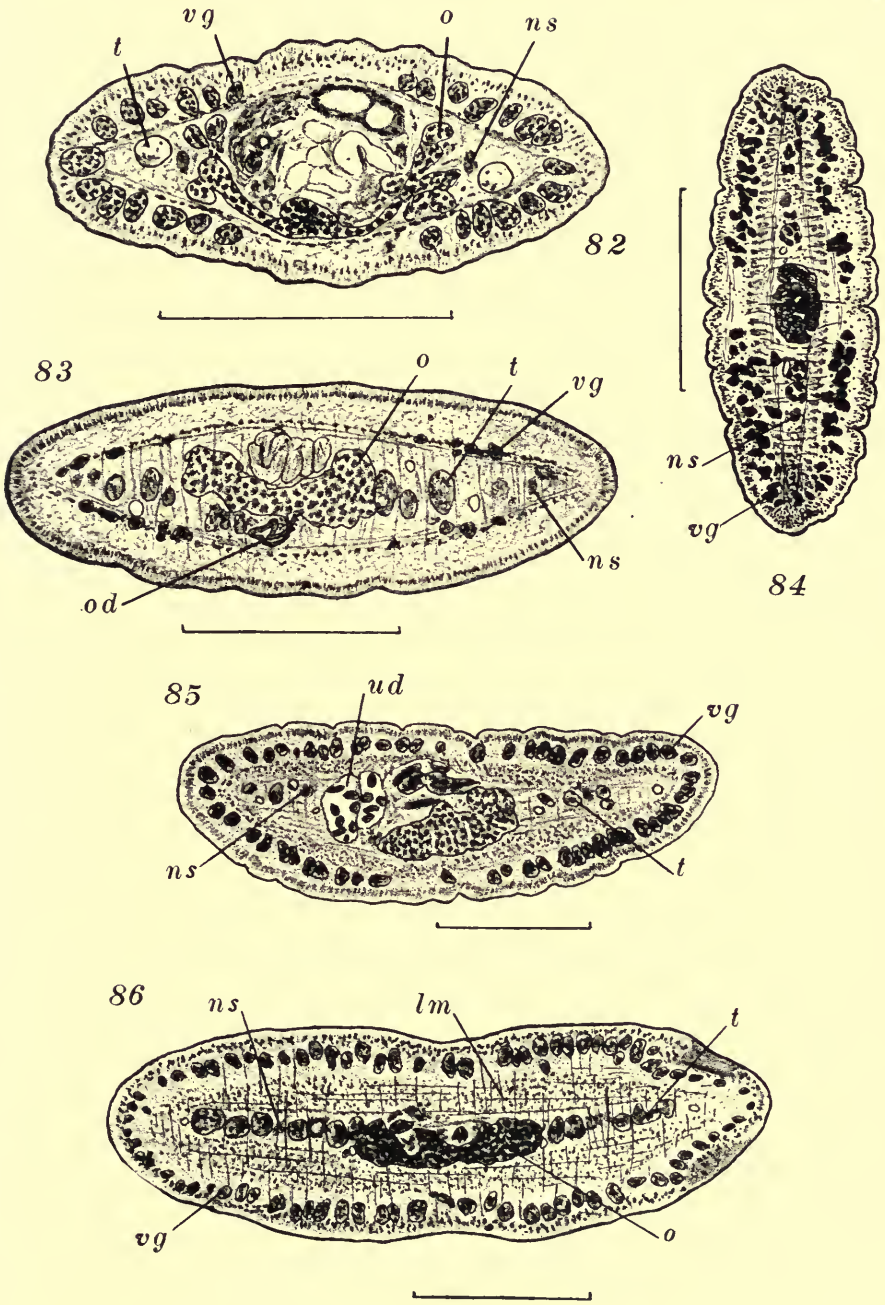
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PLATE X

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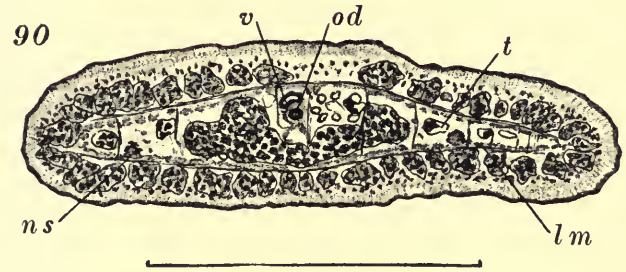
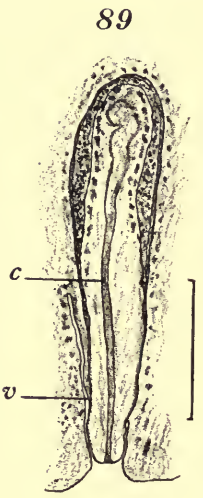
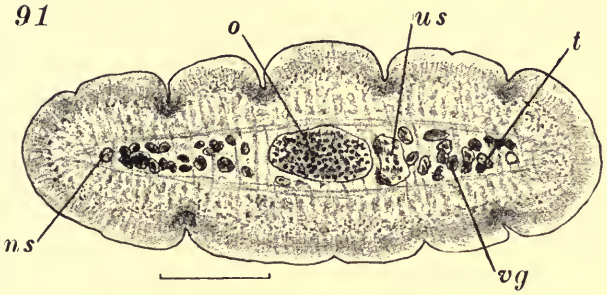
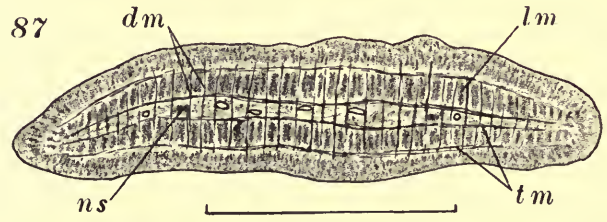
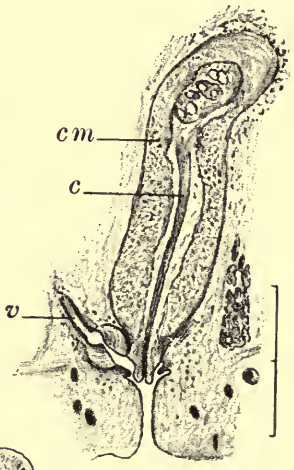
Fig. 87. *Bothriocephalus manubriformis*, transection thru anterior region.
Fig. 88. *Bothriocephalus manubriformis*, cirrus-sac and vaginal bulb from a transection.
Fig. 89. *Bothriocephalus occidentalis*, cirrus-sac from a transection. The reference line is 0.1mm. long.
Fig. 90. *Clestobothrium crassiceps*, transection thru the ovary.
Fig. 91. *Abothrium rugosum*, transection thru the ovary.
Fig. 92. *Abothrium crassum*, transection thru the ovary of a specimen from *Salmo salar*.











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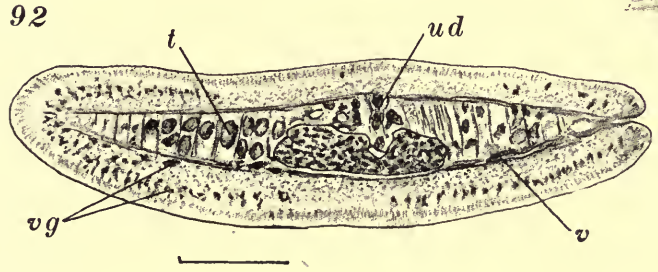
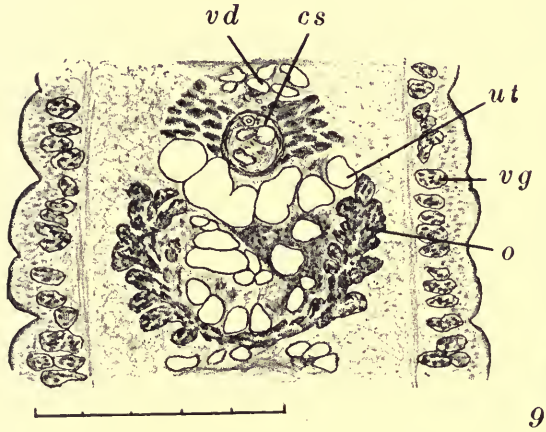


PLATE XI

EXPLANATION OF PLATE

Fig. 93. *Cyathocephalus americanus*, frontal section of ripe proglottis.
Fig. 94. *Bothrimonus intermedius*, median sagittal section.
Fig. 95. *Bothriocephalus scorpii*, median sagittal section, composite. The reference line is 0.3mm. long.
Fig. 96. *Bothriocephalus claviceps* from *Eupomotis gibbosus*, median sagittal section.
Fig. 97. *Bothriocephalus manubriformis*, transection thru uterus opening.



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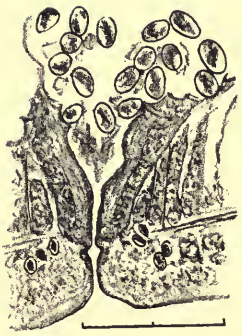

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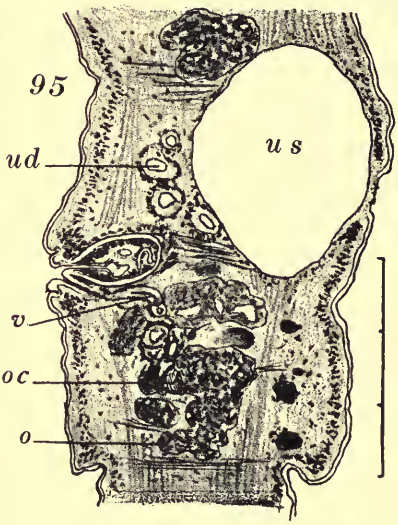

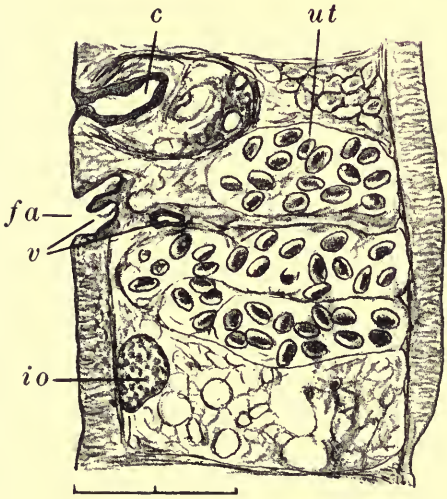

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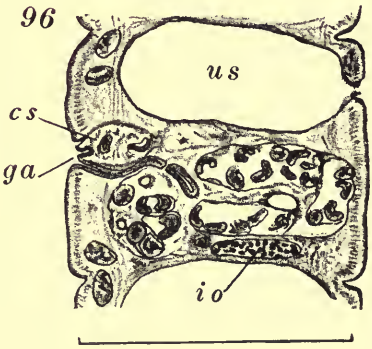

PLATE XII

EXPLANATION OF PLATE

Fig. 98. *Ligula intestinalis*, union of vagina and vitelline duct with oviduct. The reference line is 0.1mm. long.
Fig. 99. *Cyathocephalus americanus*, oocapt containing an ovum.
Fig. 100. *Marsipometra hastata*, genital cloaca from frontal section.
Fig. 101. *Marsipometra hastata*, cirrus sac from a transection.
Fig. 102. *Bothriocephalus cuspidatus*, median sagittal section, composite.
Fig. 103. *Clestobothrium crassiceps*, median sagittal section, composite.

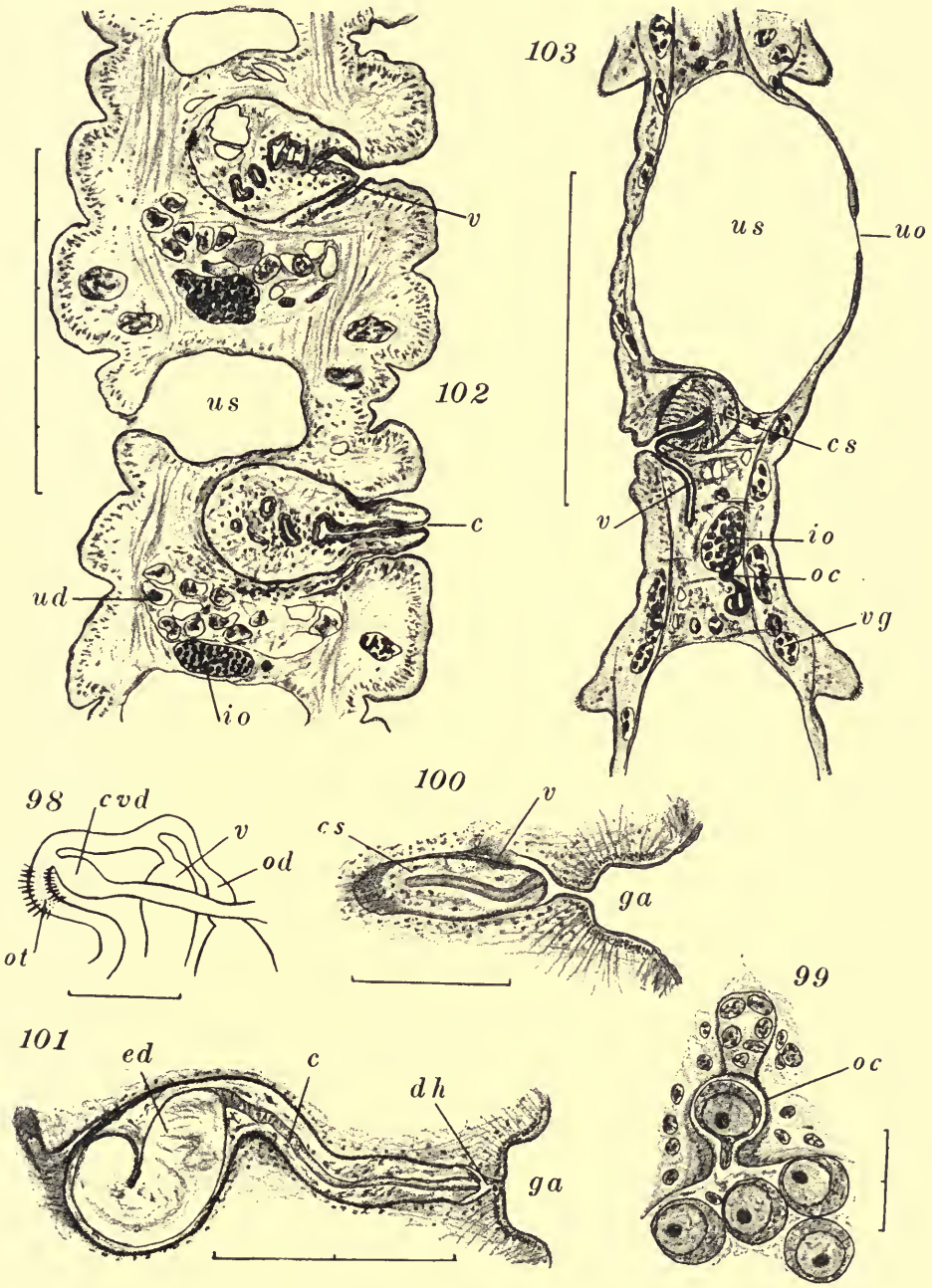
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PLATE XIII

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Fig. 104. *Cyathocephalus americanus*, diagram of median sagittal section.

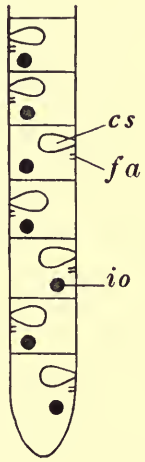
Fig. 105. *Bothriocephalus scorpii*, portion of section, showing union of vagina with oviduct.

Fig. 106. *Bothriocephalus cuspidatus*, young egg, showing an early stage in development, drawn from life.

Fig. 107. *Bothriocephalus cuspidatus*, older egg, many-celled stage.

Fig. 108. *Clestobothrium crassiceps*, four consecutive sections thru union of vagina and oviduct, showing the receptaculum seminis.

Fig. 109. *Abothrium rugosum*, union of vagina and common vitelline duct with oviduct. The reference line is 0.02mm. long.



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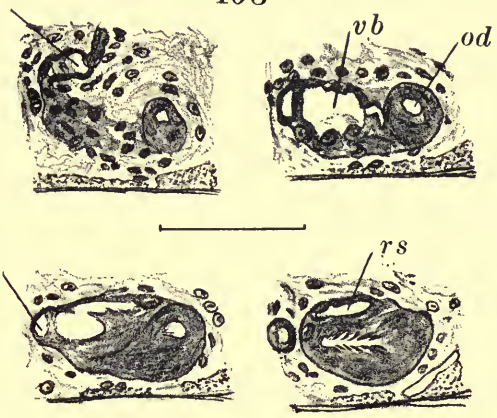

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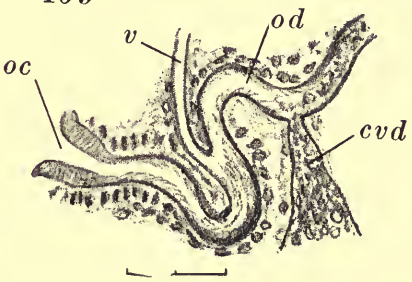

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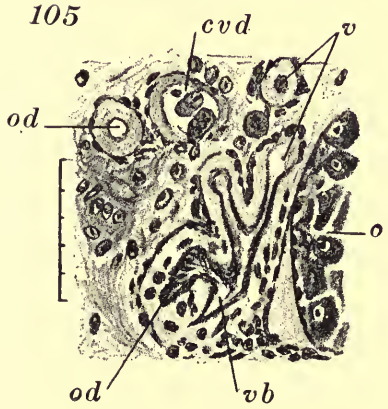

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